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INHERITANCE OF NUMBER OF FEATHERS OF THE FANTAIL PIGEON

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SEVERAL years ago I began to study the inheritance of the number of the tail feathers in fantail pigeons, partly because of a challenge that I would not recover the fantail in the F_2 generation, the implication being that the inheritance was not Mendelian. The race of fantails is a very old one and the pigeons have been very intensively selected by fanciers for many years. It was therefore to be expected that several modifications had in time been accumulated in the direction of selection. Nevertheless, it was to be expected that if a sufficient number of individuals were bred, the original type would reappear. If two factors in homozygous condition are essential for the reappearance in F_2 of the original fantail, then such an individual is expected once in sixteen cases; if three factors, once in sixty-four cases; if four, once in two hundred and fifty-six; if five, only once in 1,048 cases, etc. This relation holds if the fantail factors are all recessive, but fewer factors are called for if one or more of them is dominant, and the question will be still more complicated if the highest reaches of the variation are due to modifying factors acting only in the presence of other factors.

It seemed unlikely, however, that the situation would be found to be as simple as this; for, in the first place, there is no fixed number of tail feathers characteristic of

the fantail; selection of these birds has not been made exclusively in regard to number of feathers, but in regard also to their size and shape, their regularity of distribution, their method of spreading, etc. It was a priori unlikely that the race itself is homozygous for *all* of the factors that influence the number of feathers. How far the results would depend on whether the maximum effects are produced by a homozygous condition in several of the factors, with heterozygous condition in others, would be a point not easy to ascertain in a race that produces as few offspring as does the pigeon. Nevertheless, the results give, I believe, pretty clear indications that the effects are due to several factors, and they indicate, moreover, that the failure to recover the extreme type of the fantail in F_2 is probably only a question of insufficient numbers—in fact, the fantail type has probably reappeared in F_2, though not in its most extreme form, even with the relatively few F_2 pigeons that I have been able to get.

The work has extended over several years, owing to lack of suitable quarters in which to keep the birds and of assistance to take care of them. They had to be removed to and from Woods Hole each year, with the consequent loss of young and disturbance of the regularity of habits essential to a bird as conventional as the pigeon.

The original stock was obtained from Dr. F. D. Solley, of New York City, a well-known breeder of high-grade fantails. Dr. Solley has also supplied me with information as to the number of tail feathers in birds of his strain. Unfortunately these numbers were not obtained until a year after these particular birds had passed out of his hands. He assures me they are typical, and the birds of his stock that I saw when my parent birds were obtained were closely similar in tail number, etc., to those here recorded.

The birds with which the original fantails were bred to get F_1 stock were ordinary birds. As they were not pedigreed stock there is a small chance that they might have contained factors of the fantail type, but this is

highly improbable, since they had the number of feathers characteristic of nearly all other strains of pigeons, and especially of the more common ones.[1] Three P_1 pairs were used (two male fantail and one female) but the F_1 individuals were not kept apart (for want of space) and, as no marked difference appeared amongst the F_1 progeny when the fantail parent was female or male, the F_1's from the reciprocal crosses were mixed together. This is unfortunate, for fuller and more accurate observations might have revealed significant differences indicative of sex-linked factors. I can only state that if such are here involved their effect is slight, and was not observed at the time when the two kinds of F_1 offspring were reared.

History of the Fantail Race

In his book on "Animals and Plants under Domestication" Darwin has given a great deal of important information about the origin and characteristics of the fantail.

> "The normal number of tail feathers in the genus *Columba* is 12; but fantails have from only 12 (as has been asserted) up to, according to MM. Boitard and Corbie, 42. I have counted in one of my own birds 33, and at Calcutta Mr. Blyth has counted in an *imperfect* tail 34 feathers. In Madras, as I am informed by Sir W. Elliot, 32 is the standard number; but in England number is much less valued than the position and expansion of the tail. The feathers are arranged in an irregular double row; their permanent fan-like expansion and their upward direction are more remarkable characters than their increased number. The tail is capable of the same movements as in other pigeons and can be depressed so as to sweep the ground. It arises from a more expanded basis than in other pigeons; and in three skeletons there were one or two extra coccygeal vertebræ. I have examined many specimens of various colors from different countries, and there was no trace of the oil gland; this is a curious case of abortion.[2] The neck is thin and bowed backwards. The breast is broad and protuberant. The feet are

[1] At least one other of the domesticated races may have more than twelve feathers in the tail.

[2] "This gland occurs in most birds; but Nitzsch (in his 'Pterylographie,' 1840, p. 55) states that it is absent in two species of *Columba*, in several species of *Psittacus*, in some species of *Otis*, and in most or all birds of the Ostrich family. It can hardly be an accidental occurrence that the two species of *Columba* which are destitute of an oil gland have an unusual number of tail feathers, namely 16, and in this respect resemble fantails."

small. The carriage of the bird is very different from that of other pigeons; in good birds the head touches the tail feathers, which consequently often become crumpled. They habitually tremble much; and their necks have an extraordinarily, apparently convulsive, backward and forward movement. Good birds walk in a singular manner, as if their small feet were stiff. Owing to their large tails, they fly badly on a windy day. The dark-colored varieties are generally larger than white fantails."

"Mr. Swinhoe sent me from Amoy, in China, the skin of a fantail belonging to a breed known to have been imported from Java. It was colored in a peculiar manner, unlike any European fantail; and, for a fantail, had a remarkably short beak. Although a good bird of the kind, it had only 14 tail feathers; but Mr. Swinhoe has counted in others of this breed from 18 to 24 tail feathers. From a rough sketch sent to me, it is evident that the tail is not so much expanded or so much upraised as in even second-rate European fantails. The bird shakes its neck like our fantails. It had a well-developed oil gland. Fantails were known in India, as we shall hereafter see, before the year 1600; and we may suspect that in the Java fantail we see the breed in its earlier and less improved condition." Vol. I, Chap. V, p. 153.

"The first notice of the existence of this breed is in India, before the year 1600, as given in the "Ayeen Akabery"; at this date, judging from Aldrovandi, the breed was unknown in Europe. In 1677, Willighby speaks of a fantail with 26 tail feathers; in 1735, Moore saw one with 36 tail feathers; and in 1824, MM. Boitard and Corbie assert that in France birds can easily be found with 42 tail feathers. In England, the number of the tail feathers is not at present so much regarded as their upward direction and expansion. The general carriage of the bird is likewise now much valued. The old descriptions do not suffice to show whether in these latter respects there has been much improvement; but if fantails with their heads and tails touching had formerly existed, as at the present time, the fact would almost certainly have been noticed. The fantails which are now found in India probably show the state of the race, as far as carriage is concerned, at the date of their introduction into Europe; and some, said to have been brought from Calcutta, which I kept alive, were in a marked manner inferior to our exhibition birds. The Java fantail shows the same difference in carriage; and although Mr. Swinhoe has counted 18 and 24 tail feathers in his birds, a first-rate specimen sent to me had only 14 tail feathers.[3]

A later statement in regard to fantails from Fulton's Book of Pigeons gives some additional details.[4]

[3] Darwin, ''Animals and Plants,'' Chapter VII, p. 218.

[4] ''The Illustrated Book of Pigeons with Standards for Judging,'' by Robert Fulton, edited by L. Wright. Cassell & Co., Ltd., New York.

The tail also is peculiar, and quite uncommon. It is long and composed of 14 to 22 feathers, 16 being about the average number in these birds; these are arranged equally on either side, one above another, and the two top ones, diverging a little outwards, show a slight division in the tail, but there is not the slightest affinity or resemblance to a "fan" tail, as some might suppose by the excessive number of feathers, but it is a distinct peculiarity of this breed (12 being the normal number of tail-quills in most pigeons). The greater the number of quills in "Oriental Rollers" the more the specimens are valued. A further singular feature noticeable in the tails of these birds is that occasionally two feathers may be found growing from one quill, separating at its pithy junction as a twin feather, each rather narrower than ordinarily, but of the usual length, and not outgrown, or causing a disordered formation of the tail (p. 195).

. . . The tail is the other chief point in the English breed. The feathers should lie flat and evenly over one another (none of them being set edgeways), so as to form a neat double row. In number they should not be less than 28, but as many more as the bird can carry nicely. The Birmingham Columbarian Society, in an article published by them some years ago, laid down 40, arranged in 3 rows, as the proper number; but though I have heard of such birds I have never seen one. I once had a hen with 38 tail-feathers. I purchased her from Mr. Fulton, and I believe she had been imported from India; and I have often bred birds with tails of 36 or 37 feathers carried in most orthodox fashion. In an exhibition pen the number is of no consequence, provided that the tail is well spread and circular, and well filled up all around; but in the breeding pen a thickly-feathered tail is of great value. In the breeding of any animal for any fancy point, if you can get that point in excess in either of the parents so much the easier is your task. You have then something to *spare,* instead of something to breed up to, which is a very different matter (p. 329).

The P_1 Generation

The three original fantails had 29, 30 and 32 tail feathers, respectively (Fig. 1). From Dr. F. D. Solley I got the records of other fantails of the same stock given in Fig. 2. The other parents were ordinary homers purchased from a breeder of these birds.

The F_1 Offspring

The numbers of tail feathers shown by the 41 individuals of the F_1 generation are recorded in Fig. 3. The range of variation is from 12 to 20, with the highest fre-

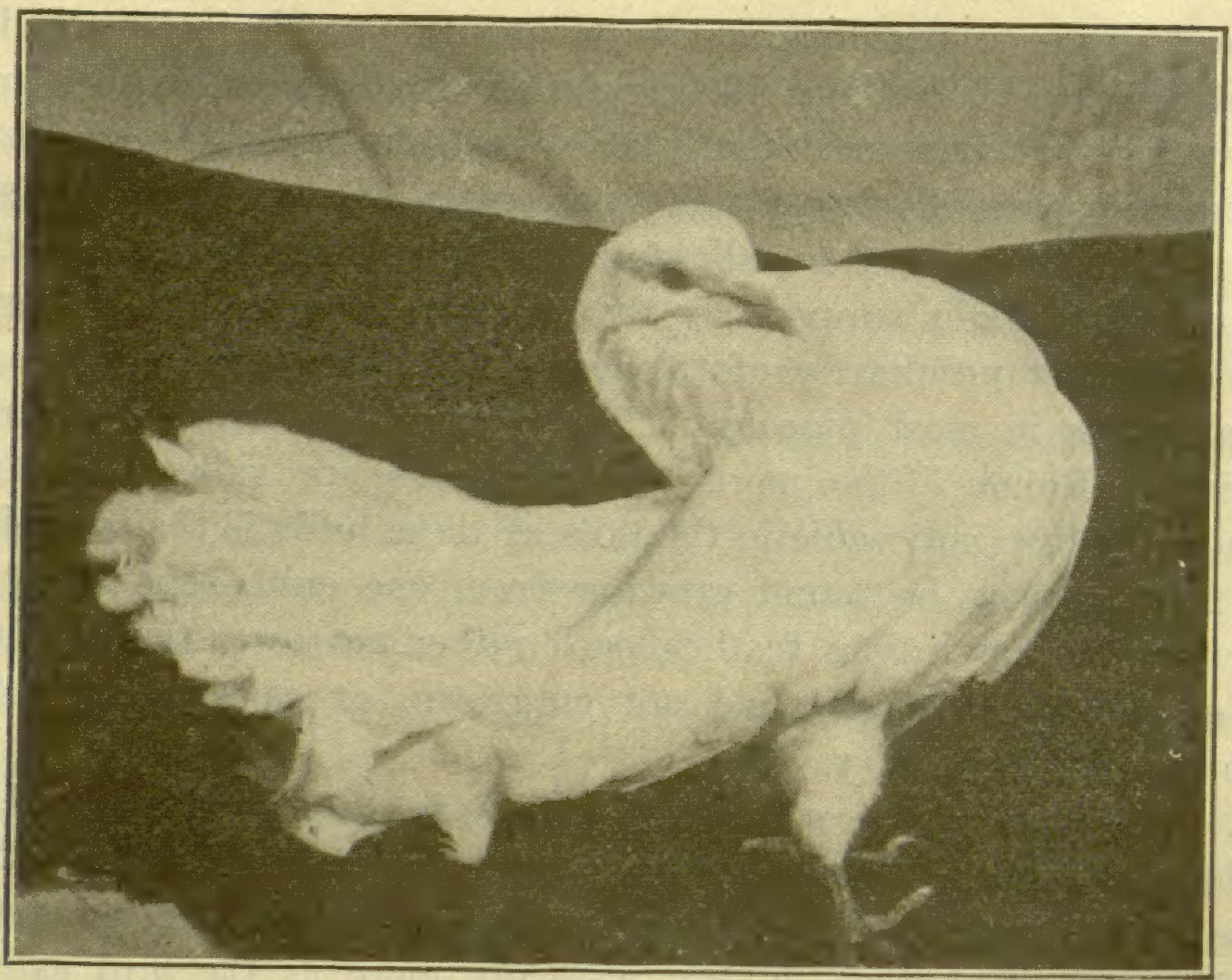

FIG. 1. One of fantail pigeons used in the experiments.

quency in the 14-tail-feather class. Evidently one or more of the factors of the fantail act as partial dominants, producing tails that have for the most part more tail feathers than has the common pigeon but less than the fantail. In appearance these F_1 birds are more like the common pigeon, having lost the peculiar carriage

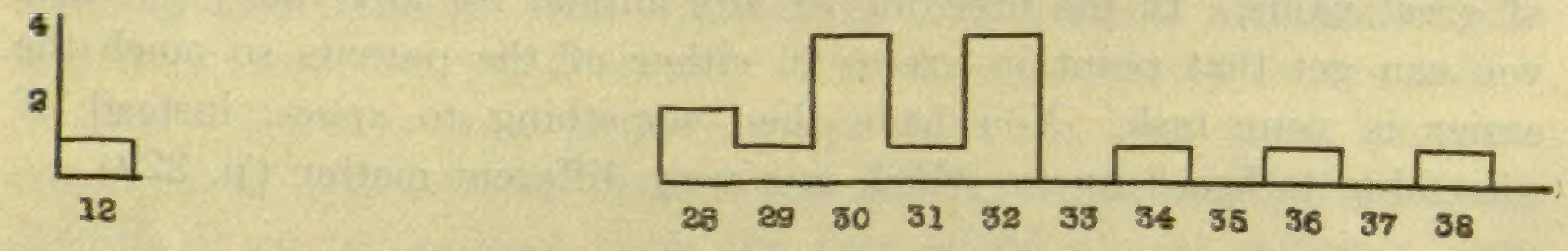

FIG. 2. Frequency distribution of tail feathers in parent "homers" (left), and fantails (right).

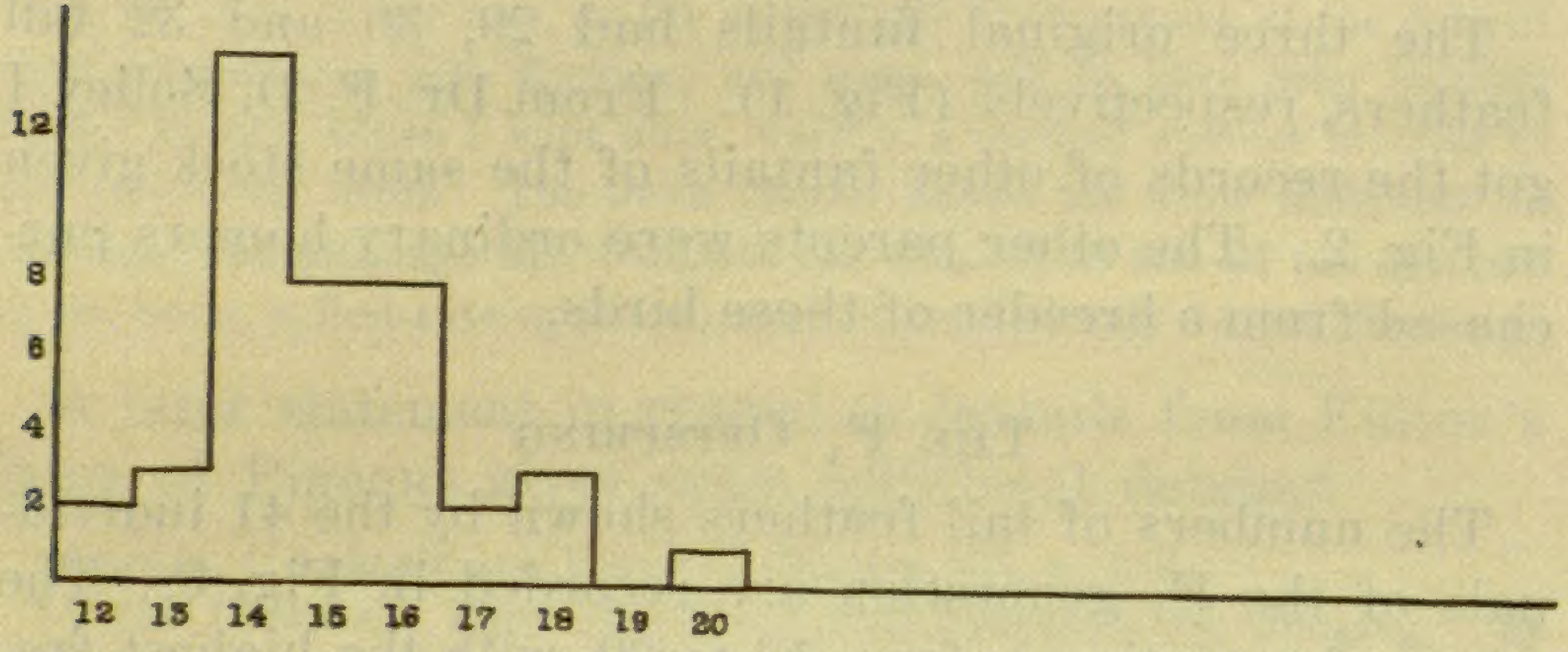

FIG. 3. Frequency distribution of tail feathers in F_1.

of the fantail and its peculiar shape. The tail is, however, often wedge-shaped instead of flat as in ordinary birds. There were 28 birds with an even number of

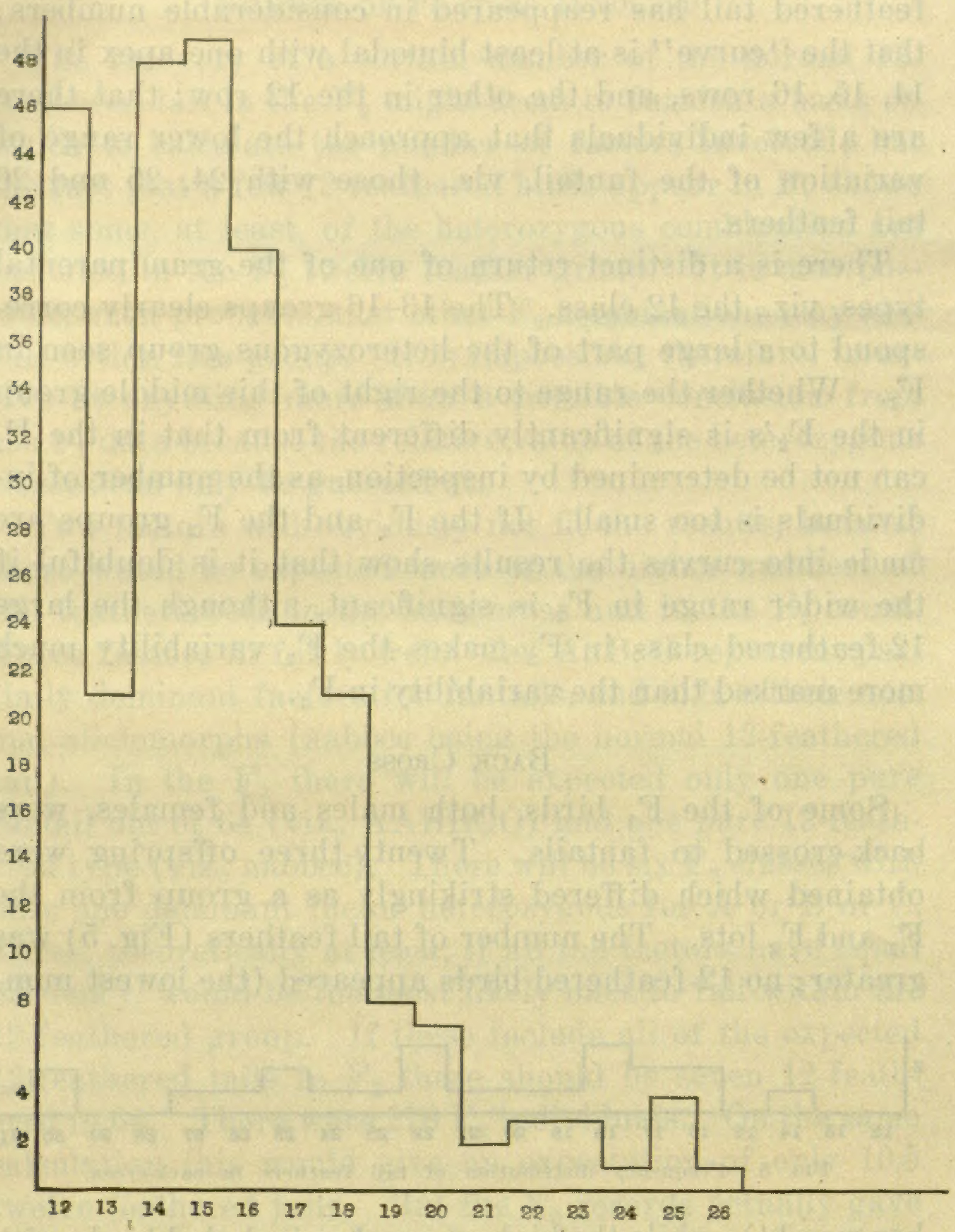

FIG. 4. Frequency distribution of tail feathers in F_2.

feathers and 13 with an odd number—a considerable preponderance of even number of feathers. Of the 41 individuals, 30 are included in the classes with 14, 15, 16 tail feathers.

THE F_2 GENERATION[5]

A glance at Fig. 4 shows that the range of variation of the F_2 group is greater than that of the F_1; that the 12-feathered tail has reappeared in considerable numbers; that the "curve" is at least bimodal with one apex in the 14, 15, 16 rows, and the other in the 12 row; that there are a few individuals that approach the lower range of variation of the fantail, viz., those with 24, 25 and 26 tail feathers.

There is a distinct return of one of the grandparental types, viz., the 12 class. The 13–16 groups clearly correspond to a large part of the heterozygous group seen in F_1. Whether the range to the right of this middle group in the F_2's is significantly different from that in the F_1 can not be determined by inspection, as the number of individuals is too small. If the F_1 and the F_2 groups are made into curves the results show that it is doubtful if the wider range in F_2 is significant, although the large 12-feathered class in F_2 makes the F_2 variability much more marked than the variability in F_1.

BACK CROSS

Some of the F_1 birds, both males and females, were back-crossed to fantails. Twenty-three offspring were obtained which differed strikingly as a group from the F_1 and F_2 lots. The number of tail feathers (Fig. 5) was greater; no 12-feathered birds appeared (the lowest num-

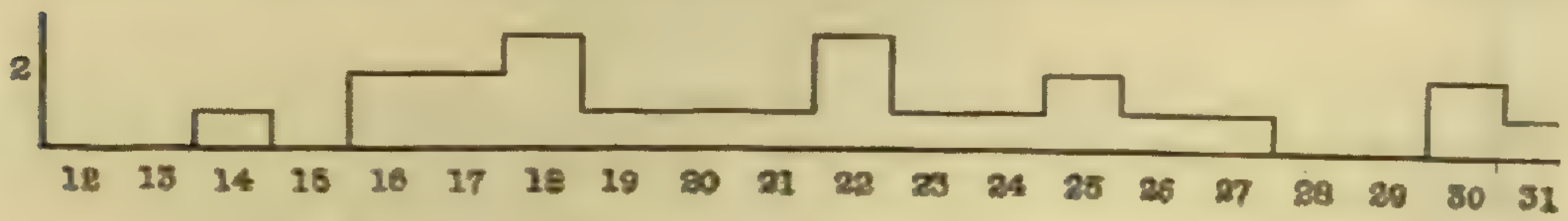

FIG. 5. Frequency distribution of tail feathers in back-cross.

ber was 14); while the highest number included birds with 30 and 31 tail feathers. The latter would undoubtedly pass-for-fantail, so far as the number of tail feathers was

[5] There are some discrepancies between the F_2 and back-cross tables given here and the records of the groups given in "The Mechanism of Mendelian Heredity." The present account is more accurate, as some of the former data was obtained from the birds while still alive.

concerned. The carriage of most of the birds was noticeably much more like the fantail than that of the F_1 and F_2 birds.

Number of Factors Involved

The recovery of a certain number of the normal 12-feathered tail in the F_2 might seem to furnish a basis on which to calculate the number of factors involved; but the fact that a few 12-feathered birds appear in F_1 shows that some, at least, of the heterozygous combination are included in the F_2 twelve feather group. It is also possible, even probable, that other F_2 combinations may also fall within this group. It is impossible, therefore, to arrive at anything more than a possible conclusion from the F_2 data because the relative value of the heterozygous classes can only be guessed at.

Two factors will obviously not fit the results, because there would be expected more of the higher numbers of tail feathers both in the back cross and in the F_2 count. Three factors fit fairly well. Let A, B, C represent partially dominant factors for fantails, and a, b, c their normal allelomorphs (aabbcc being the normal 12-feathered tail). In the F_2 there will be expected only one pure fantail out of 64 (viz., AABBCC) and one *pure* 12-feathered type (viz., aabbcc). There will be six F_2 classes with only one dominant factor heterozygous for A or B or C. These, theoretically at least, if all the factors have equal efficiency, would be the most likely ones to fall within the 12-feathered group. If these include all of the expected 12-feathered tails in F_2 there should be seven 12-feathered in 64. There were 278 F_2 individuals. On the same calculation this would give an expectation of only 10.5 twelve-feathered tails. But the F_2 records actually gave 46 normal tails. Obviously still other combinations realized in F_2 must come under this class. It would be mere guesswork to try to state which are the more probable combinations.

The back cross furnishes data that permit a better means of calculation. Here eight kinds of germ cells and eight

zygotes are expected on the assumption of a three-factor cross, viz.,

ABC	ABc	Abc	aBC	abC	aBc	abc
abc	abc	abc	abc	abc	abc	abc

Of these eight kinds of individuals, some of only one class, might be expected to be wild type (viz., of class abcABC) in the sense that individuals of this class correspond in formula to the F_1 offspring, and, of these F_1 offspring, 2 out of 41 have tails with 12 feathers, or 1 in 20. Amongst the 24 back crossed individuals, there were none with 12 feathers only and at most one is expected. If we assign to the group of abcABC also the four individuals of the back cross in the 14 and 16 groups, and assign the 3 individuals of the 30 and 31 groups to the pure fantails, there remain 17 individuals in the middle range that belong to the six intermediate groups that are homozygous in one or in two fantail modifiers. There are six intermediate classes between the end classes just spoken of. If we are right in the limits assigned to the end classes, the expectation would be 18 individuals for the intermediate classes, where 17 are so classified, which is also not a bad fit.

Four factors fit the data about as well as three,[6] but if three will suffice the smaller number is perhaps preferable. It is evident that the data do not allow close analysis, but only because they are not sufficiently large, especially in the back cross. Nevertheless, it is important to find out that, so far as the results go, they are not unconformable with the Mendelian assumption of segregation of a few pairs of factors.

LINKAGE

When all F_2 tails that are blue are classified they fall into the groups shown in Fig. 6; similarly, the white tails

[6] On this assumption relatively fewer fantails are expected in F_2, which is a better fit, but fewer also in the back cross, which apparently is not so good a fit. The proportion would also depend, however, on the relative efficiency and the completeness of the dominance of each factor. The above evidence proves that there must be at least three factors.

give the groups shown in Fig. 7. A comparison of these groups shows that there is a relatively large number of high-feathered tails amongst the whites, while among the

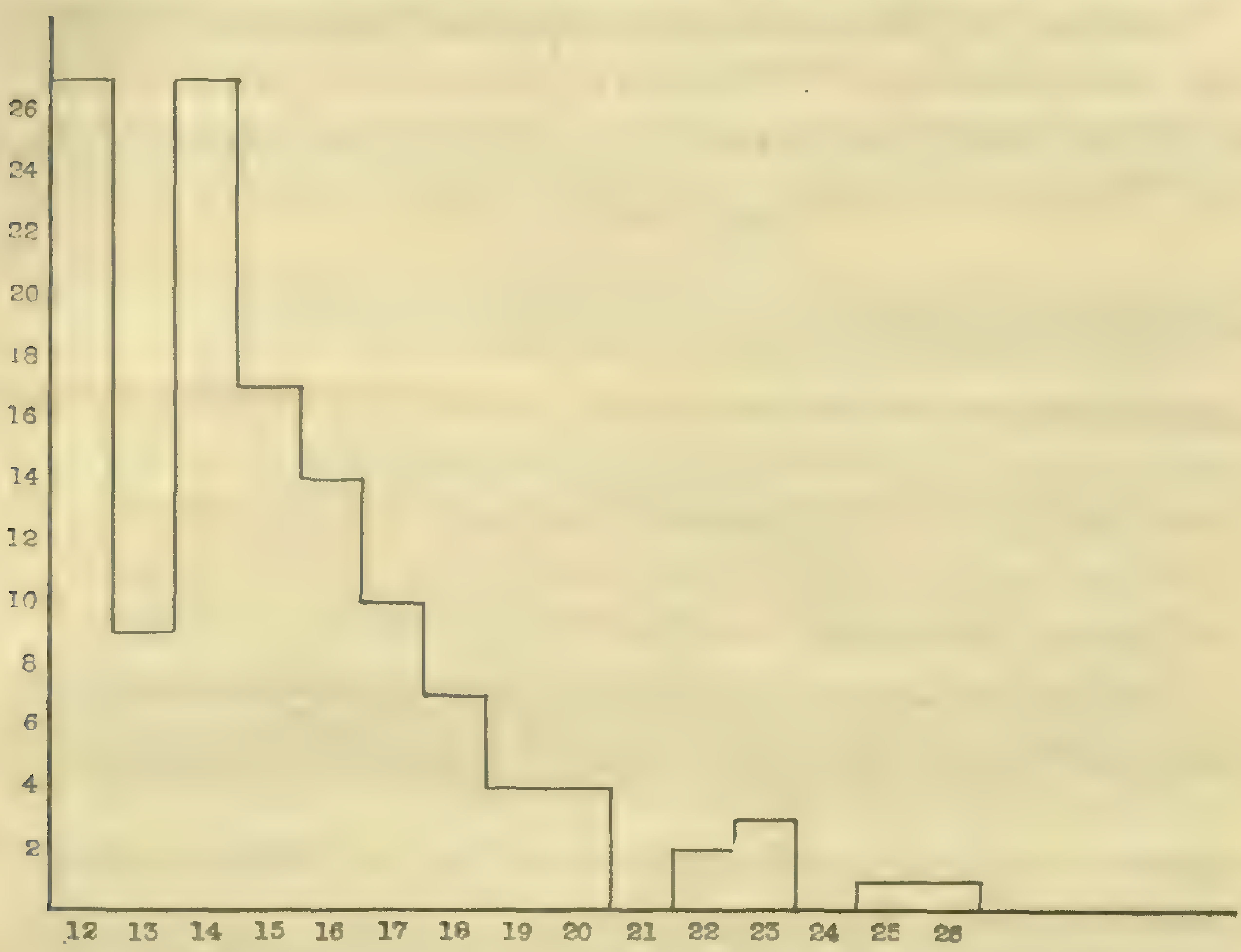

FIG. 6. Frequency distribution of blue tail feathers in F_2.

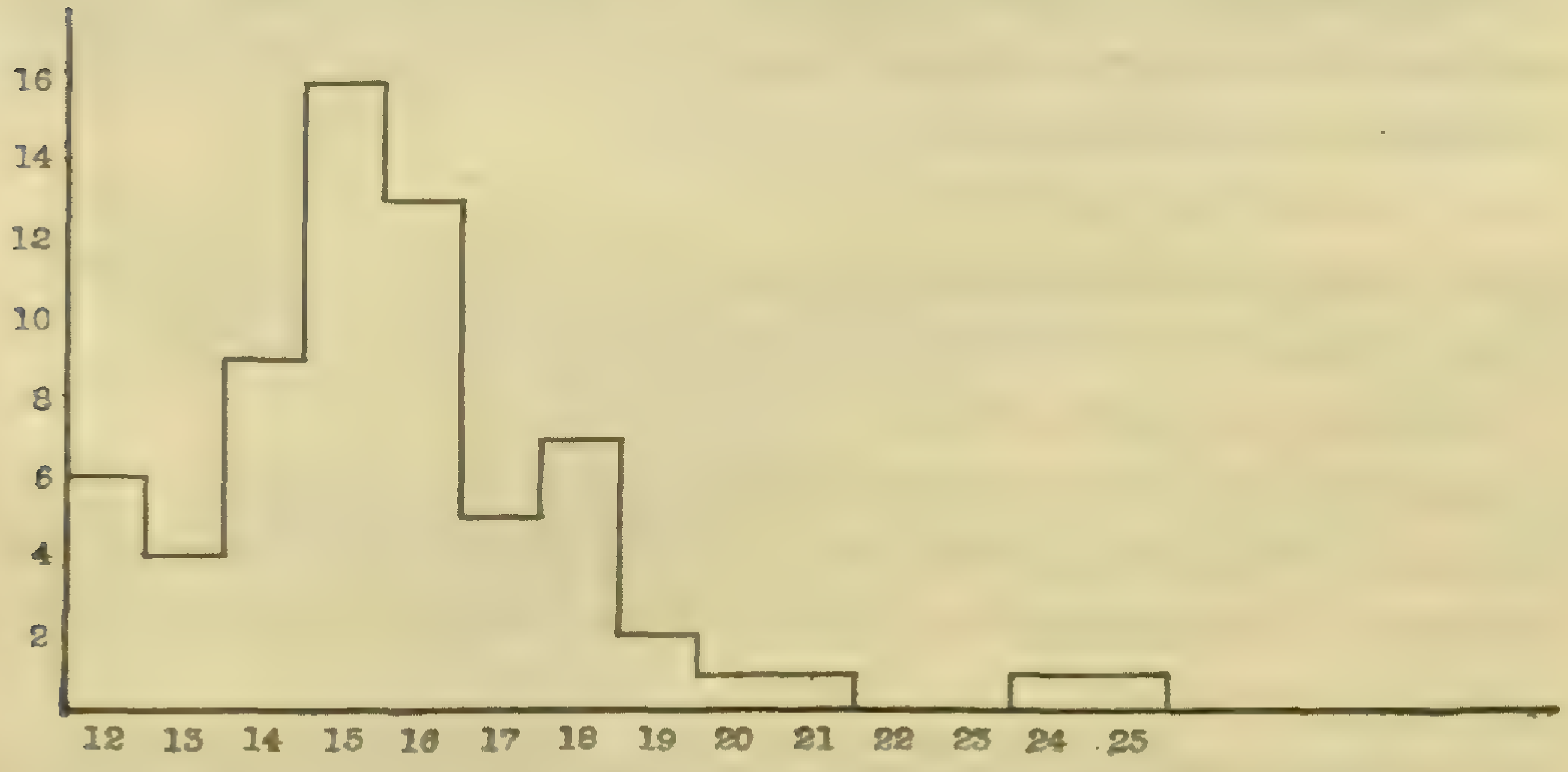

FIG. 7. Frequency distribution of white tail feathers in F_2.

blues, the 12-feathered tails are relatively more frequent. A not improbable interpretation of this relation is that the principal factor for white is linked to one or more of the factors for increased number of feathers.

Since these results occur in the F_2 count, it is unfortunately not possible to deduce from them whether crossing over takes place in one or both or neither sex.

Amongst the tails were some that had both blue feathers and white feathers. These give the group shown in Fig. 8, which closely corresponds to the blue-tail group (Fig. 6). There were other tails with white feathers having

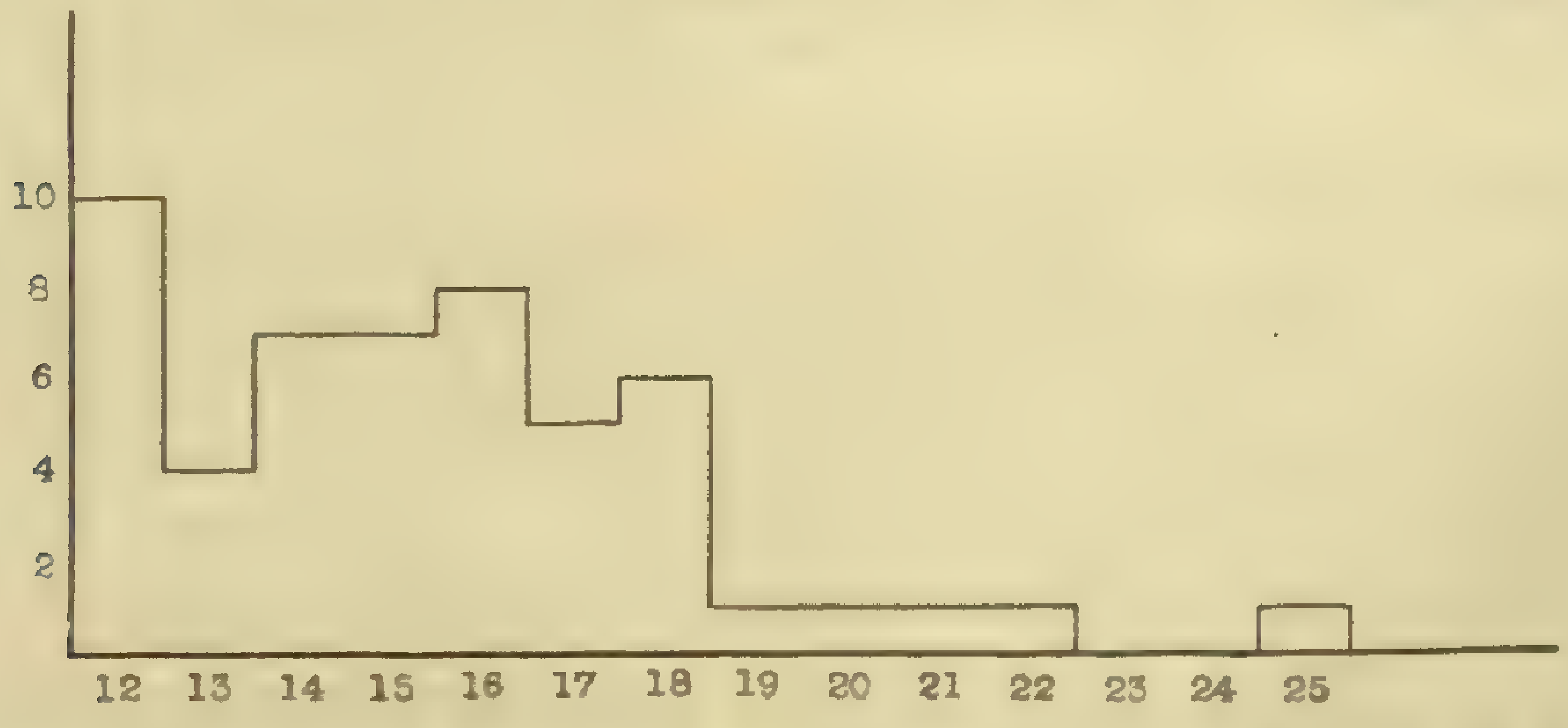

FIG. 8. Frequency distribution of blue-and-white tail feathers in F_2.

pigment along the margins as in Fig. 15. These, when classified, gave the group shown in Fig. 9, which apparently is the same as the group of white tails (Fig. 7).

The number of birds in the F_1 and in the back cross are too few to give significant results when broken up into the two groups of white or blue.

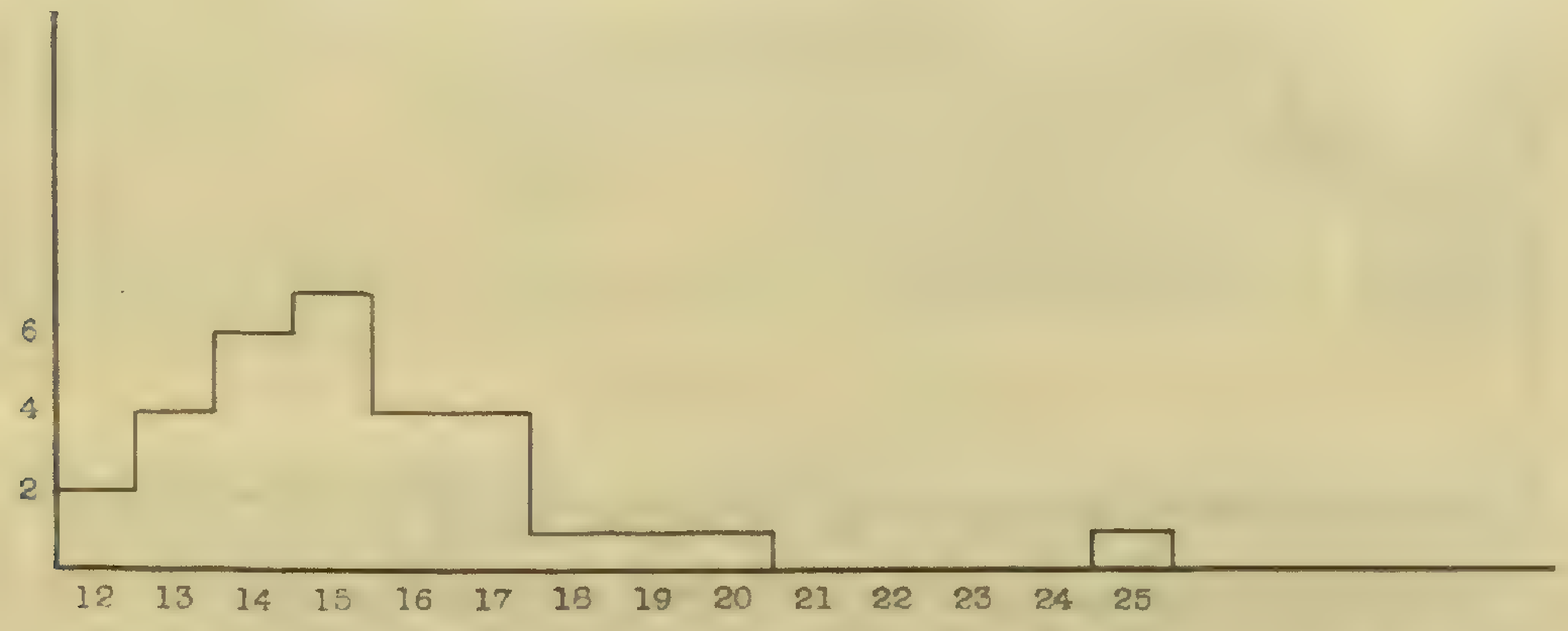

FIG. 9. Frequency distribution of "edged white" tail feathers in F_2.

The tails are not a complete index of the bird from which they came, for a bird with a pure white tail might have color patches elsewhere on its body; but as no rec-

ords were kept of the entire color of each bird, it is not now possible to find out how closely the complete pattern would correspond with the tail color. In general, however, in these birds the tail is a partial index, at least—a fair sample, perhaps—of the entire color.

"Correlation" between the Oil Gland and the Number of Tail Feathers

Darwin suggests a "correlation" between the absence of the oil gland and the increased number of tail feathers. Such a relation might be a direct correlation in the sense that the overdevelopment of the tail feathers suppresses or tends to suppress the development of the oil gland that is situated on the uropygium just above the base of the tail feathers. If this were the true interpretation of the condition in the fantail, one would expect to find in F_1 and F_2 all degrees of development of the oil gland. If, on the other hand, the absence of the oil gland is an inherited peculiarity having nothing directly to do with the number of feathers, then in the F_2 series we might expect to find a numerical relation indicating its mode of inheritance. Unfortunately the pedigrees of the normal tailed pigeons that had been mated to the fantails were unknown. While the oil glands may be occasionally absent in domesticated pigeons, it is highly improbable that any of the homers used in the experiment carried such a factor. In classifying the F_1 and F_2 birds according to the condition of the oil gland three classes were recognized. First, "double" glands, those with the right and left sides almost separate, each with a separate opening; second, "single" glands, those with the halves united more closely and with but one external outlet;[7] third, those with no oil glands. The results are given in graphs of Figs. 10–11.

The few F_1 birds available when the oil gland was studied show a wide range of variability; all but one were double, Fig. 10 (above). This doubling might be due to

[7] An intermediate stage was also noted, viz., one with two closely fused so as to make almost a single gland.

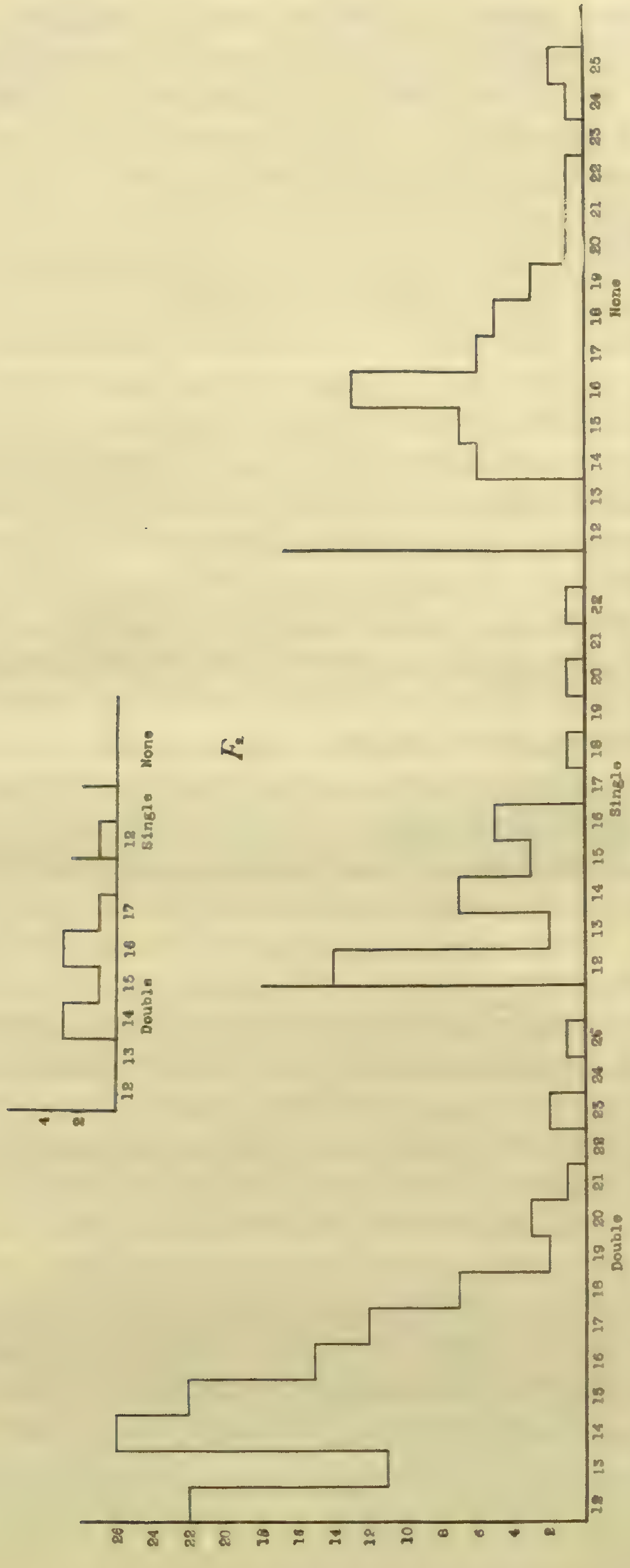

FIG. 10 (above). FIG. 11 (below). Frequency curves of occurrence of oil glands in F_1 and F_2.

partial dominance of a gene for doubling, or to a "correlation" such as Darwin spoke of, for the number of tail

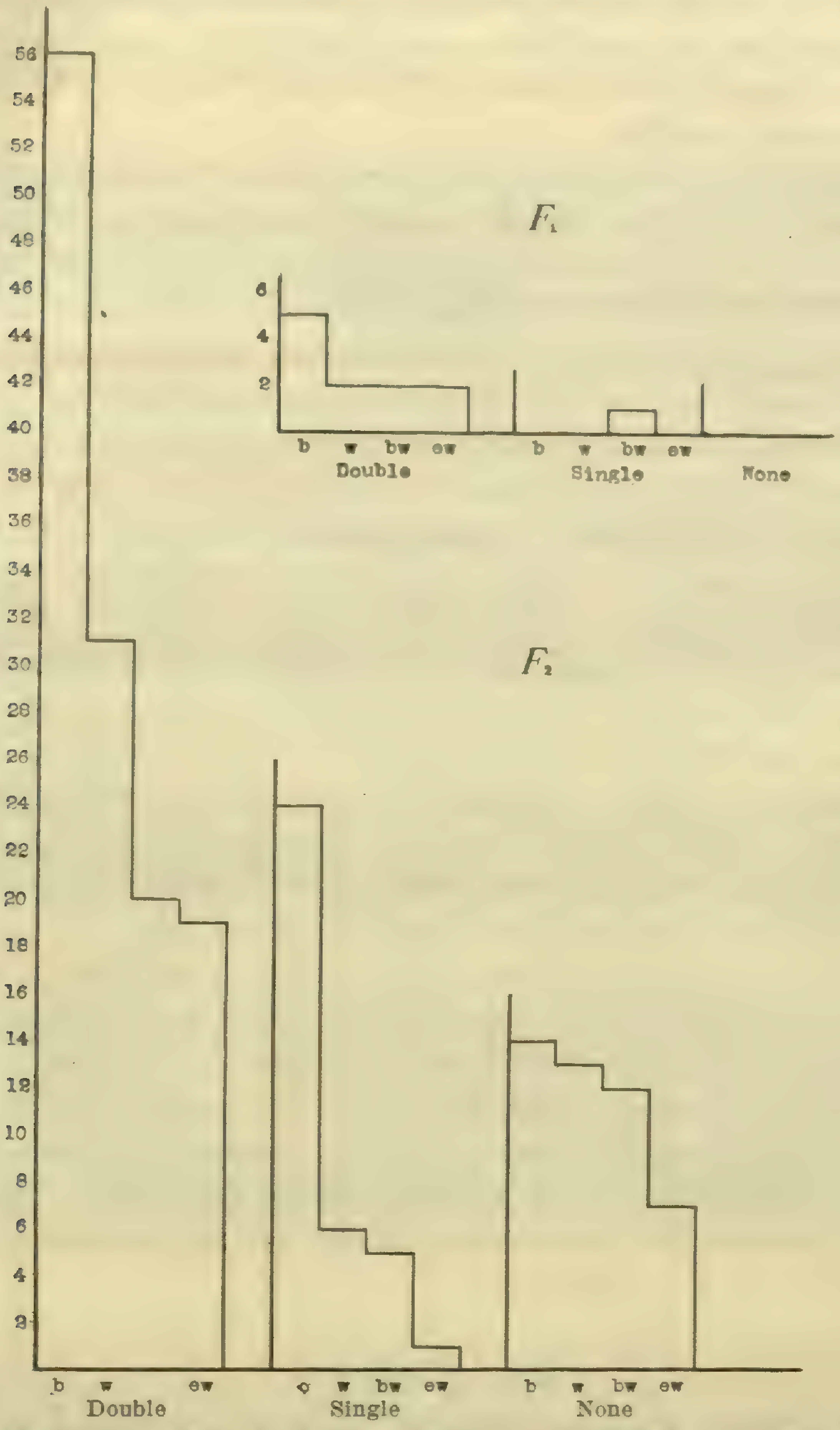

FIG. 12 (above). FIG. 13 (below). Frequency distribution of double, single and no oil glands in differently colored tails.

feathers in this particular lot was high. That the latter is probably not the explanation is shown in the F_2 birds.

The three groups of F_2 tails (Fig. 11) show 126 doubles, 36 singles, 46 none. The expectation for two factors (9:3:4), on the assumption that the doubles differ from the singles by one factor, and both from none by another factor, is 117 doubles, 39 singles, 52 none. This is not a very bad fit.

There is one striking result brought out by these curves. There are no 12- or 13-feathered birds without an oil gland. This is an expression of the relation that Darwin suggested as due to "correlation" in the sense that more tail feathers suppressed the development of the oil gland. But there is no such obvious solution as is shown by the F_2 group, for there may be a large number of tail feathers present and the oil glands be well developed, single or double. The curves suggest, rather, linkage between a gene for extra feathers, and a gene for absence of oil glands.

The tails with double, single and no oil glands were also classified according to the four color groups already referred to, viz., blue, white, blue and white, edged white (Figs. 12 and 13). The double and single curves appear to be the same, the no oil gland curve seems significantly different. If so, it means that there is some linkage between white color and absence of oil glands.

The foregoing evidence makes probable the view that a gene for more than 12 feathers, and the gene for no oil gland, and a gene for white color are linked, *i. e.*, are carried by the same chromosome. The genes for the oil gland and for the number of tail feathers are closer to each other than either is to the gene for white. More data, especially from back-crosses, will be necessary to establish this conclusion.

Split Feathers

Dr. Solley tells me that the split and double feather that occurs at times in the fantails is selected against. It is of not infrequent occurrence in the F_2 and back-crossed birds that I have obtained. In the records these

split feathers have been counted as *one* feather, without, however, intending to prejudice the question of the single or double nature of these feathers.

The most striking cases are like those represented in Fig. 14 (top row) and Fig. 15, where what appears to be

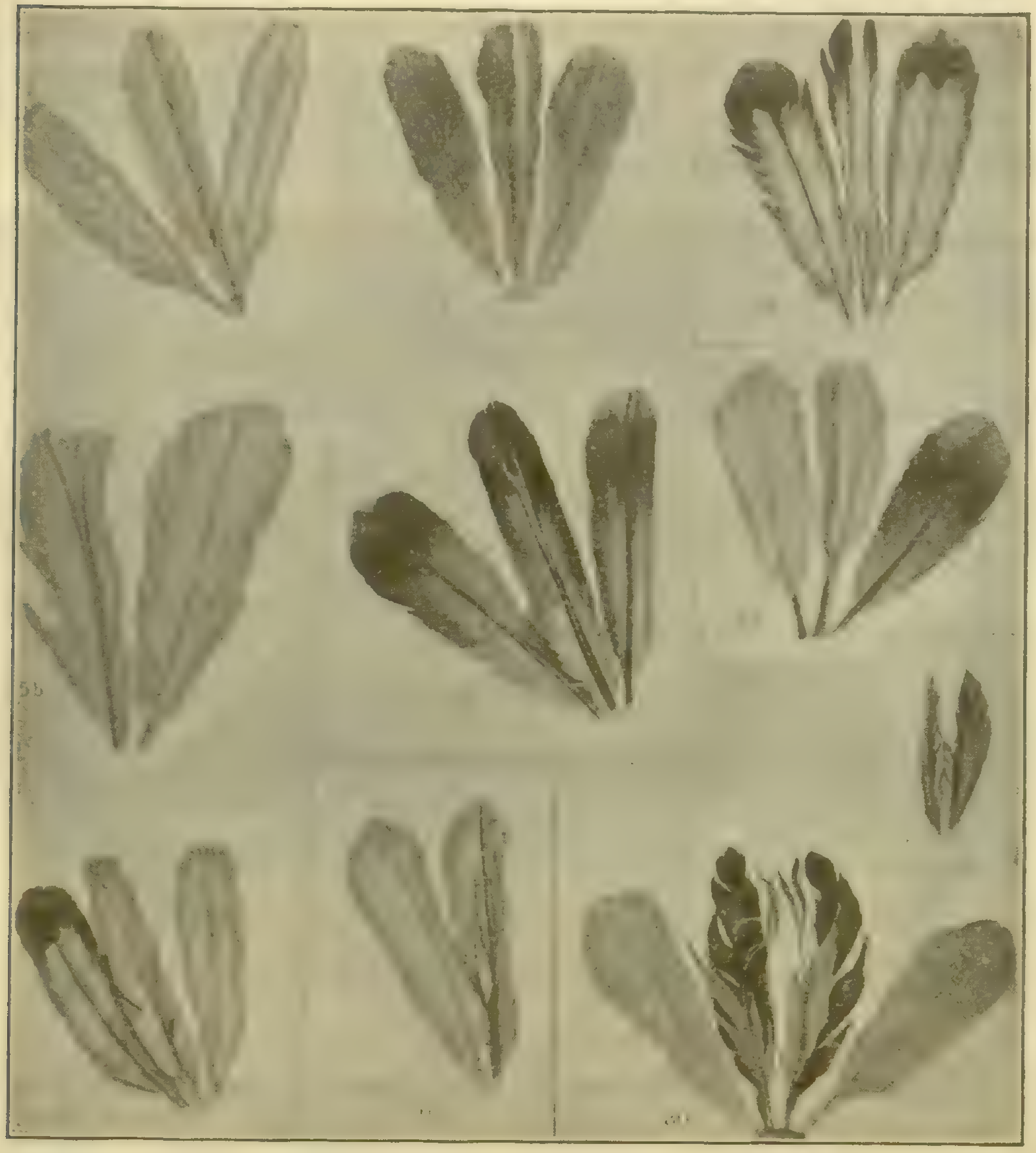

FIG. 14. Some types of split feathers.

a single feather is split in two throughout its length. While there may be a complete shaft in each half, yet the two vanes that lie on the "inner" side are not so broad as the outer half vanes, and their edges are generally frayed out and imperfectly formed. Often the vanes run across and unite the two halves.

In some of the split feathers, the division is obviously into right and left halves (Figs, 14, 15, 16); in other cases the halves make an angle with each other (Fig. 14, Nos. 37 and 80), while in still others one larger part may lie above a smaller part (Fig. 14, lowest row). Whether in the last cases the division has been in a horizontal plane, and in the first cases in a vertical one, is not certain, although the shape of the feathers even in the last case, with the imperfect edge and a narrower margin, would seem to make most probable the view that in all cases the division

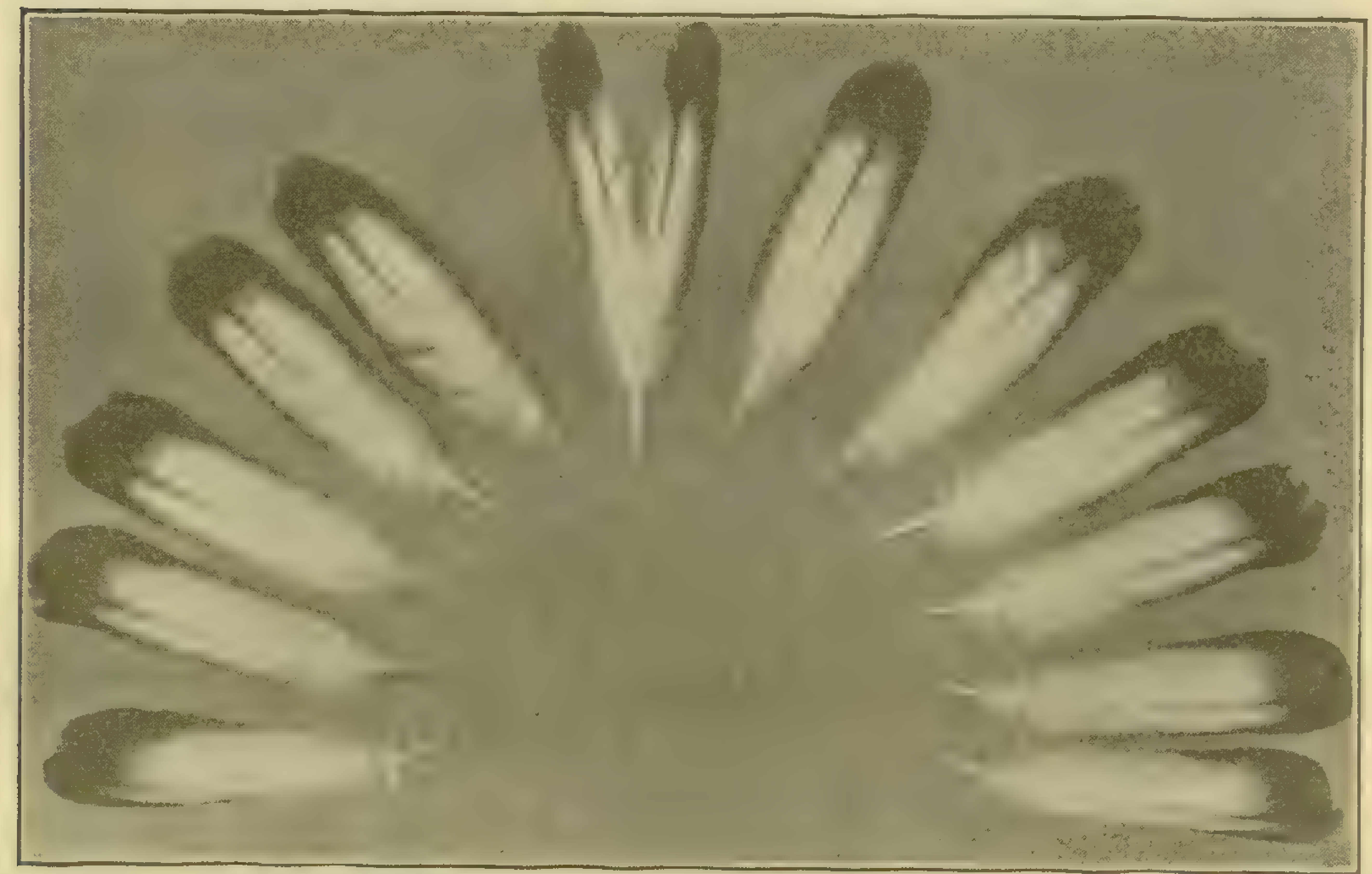

FIG. 15. An F_2 tail ("edged white") with one split feather.

has been into morphological right and left halves. The final position of the feather halves may be due to a later twisting in the sheath, or to crowding of the feathers at the base. This interpretation is further substantiated by cases in which the center of all the feathers has a white area (Fig. 14, No. 55, and Fig. 15); this is found on the imperfect side of the split feathers even when they lie one above the other. In all there were 24 F_2 tails with split feathers. Five of these had each two split feathers.

These cases grade into those in which only the distal end of the feather is split, as shown in Fig. 14, middle figure, and Fig. 16. The impression produced by feathers

of this kind is strikingly in favor of a single feather split into right and left parts at the distal end. In all, three cases of this sort were found.

To the same group are to be referred two cases, one of which is shown in Fig. 14, No. 5, *b*. Here there is a single feather, but the midrib is split near the end. The vane

FIG. 16. Split feathers with normal feathers that lie next to them.

lying between the two midribs is continuous, yet the bending inwards of this part is indicative of its dual nature.

More extreme are the eight cases of which three are shown in Fig. 16, lowest row. In all such cases there is a large, almost fully formed feather with a smaller, less perfect piece *underneath* the larger part. The first impression is that a piece has been split off the ventral side of the feather by a division in the horizontal plane. A

closer scrutiny shows, however, that the large feather is ragged along one edge only (or on a part of one edge), while the smaller piece has also on the same side (as can be seen in some cases at least) a ragged edge with the other vane more nearly complete and with a not-rough edge. It seems, therefore, more reasonable to interpret even these cases as extremes of the split-feather type in which one piece has fared worse than the other (or in which the original division was into unequal pieces).

The Size of the Double Feathers

There is a graded difference between the outer and inner vanes of the feather from the edge to the middle of the tail Fig. 15. The outer half of the vane is relatively smaller in the outermost feather, right or left, and equality of the two sides is more and more reached, the two middle feathers of the 12-feathered tails are about symmetrical. In the multiple feather tail these relations still hold, but are more difficult to trace than when the tail is simpler. It would not be profitable to attempt to analyze in detail these relations as applied to the double feathers further than to compare their surface relations with that of the feathers nearest to them or with their symmetrical mates. In all cases of split feathers the outer halves of the vanes are not so wide as is expected from the nearest feathers (or their symmetrical mates as seen in Figs. 14–16). The middle part is, as a rule, very much less than a right or left vane. The total width of the split feather is, as nearly as I can judge, about the same as the expected feathers for that position. The impression indicates that the sum of the four vanes is a little greater than the sum of the two normal vanes, but there can not be much difference as measurements show. The looseness of the frayed inner edge makes it difficult to get a very close estimate of the actual relations.

The general conclusion is that we are dealing with a single rudiment that has split at a very early stage into two parts that have completed themselves as whole

feathers, so far as this intimate union in the middle line of the bud permitted. There are no indications that the split feather is due to the union of two separate rudiments that have been pressed together so closely as to interfere with the full development of each when they came in contact.

The Location of the Split Feathers

The location of the split feathers (and modified types) is given in the next table.

Feather "split" . . .	9 near middle,	1 one quarter from side
End only split	2 near middle,	1 one third from side
Double vein at tip . .	2 near middle	
Very unequal parts .	7 near middle,	1 two thirds from side, 1 outermost feather.

In the great majority of cases the doubling occurs near the middle of the tail. The meaning of this is not at all apparent. We know so little about the cause of duplication in general and about the embryological mechanism that is involved in laying down the feathers in the tail, that it is useless to speculate about the result. The evidence from experimental embryology shows unmistakably that doubling may result from a mechanical interference with the relation of the blastomeres after they have assumed a definite position in regard to each other, but there are also many other cases known where, in normal development, a part is repeated several or many times. In these cases we can as yet only surmise that the rudiments of the structure—simple cells or groups of cells—become mechanically drawn apart by the more rapid growth of surrounding parts and separated so that each gives rise to a separate organ. Split feathers, from this point of view, would be looked upon as an incomplete separation of certain of the rudiments. However this may be, one can imagine other ways by which a specialized group of cells could become broken up into islands.

OTHER CHARACTERS IN THE CROSS

Three other characters are conspicuously present in the fantails besides the tail, viz., the white plumage, the carriage of the bird, and the shaking of the head and neck. The dominance—incomplete—of the white of the fantail was noted,[8] but the mixtures that appeared both in F_1 and F_2 make it probable that the results are not due to a single factor. The extraordinary position of the fantail pigeon with its head thrown back until it touches the tail feathers appears also to be due to at least as many factors as is the number of feathers in the tail; for it was not recovered in any of the F_2 birds, although in the back cross there were birds that showed some approach to the fantail posture. The shaking of the head disappeared in F_1 and indications of it were seen occasionally in F_2 and especially in back crosses. The character is of such a kind that its study is difficult, and it may well be an expression of some structural modification of the body rather than any direct psychological factor.

CASTRATION OF MALE

The absence of marked secondary sexual characters in the male, characters that are so conspicuous in many other birds, suggested the possibility that here, as in the Sebright male fowl, the suppression of the male plumage might be due to substances developing in the testes. Unlikely as this seemed (because pigeons with diseased testes would probably have occurred and any change recorded), nevertheless I tried the effect of castration on one young F_2 male that was just weaned. Some feathers were removed at the same time. The bird was kept for about five months and did not show any change in its plumage. It appears probable, then, that there are no genetic factors in pigeons, like those in the Sebright, which, acting through the testes, suppress the development of the plumage in the male.

[8] See Cole *et al.*

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A PRELIMINARY REPORT ON SOME GENETIC EXPERIMENTS CONCERNING EVOLUTION

RICHARD GOLDSCHMIDT

THE nature of the gene, the variability of factors and the effects of selection are favorite topics of recent discussion, which is well known to geneticists. The latest publications of Jennings and Castle will stir up anew the uncompromising parties and lead to new discussions. We think it advisable, therefore, to give a brief account of certain parts of a very large body of work on fundamental questions of evolution which we have carried on during the past nine years, with the collaboration of Dr. Seiler and Dr. Poppelbaum. Although some parts of the work have been finished for some years, we do not intend to publish a full account until all the details are worked out. But as certain results have already allowed us to form definite views in regard to some fundamental questions of evolution, we may present them, together with examples of the experiments in question.

The majority of the experimental work in regard to the fundamental problems of evolution has been done with domesticated animals and their mutations (rats, *Drosophila*) or with Protozoa, which present the complication of asexual reproduction. We have directed our attention to experimental analysis of such phenomena in nature, which must give basic information about evolution, and we have studied the following phenomena:

1. *The Geographic Variation of the Gypsy-moth.*—This well-defined species is spread over a great part of the globe. In different habitats, however, different races are found. How many of these exist can not be stated, but the number must be extraordinarily large, as we know but two localities where the same race is found. We have found all the races to be perfectly fertile with each other, with the exception of one combination which has never been successful. We have studied and are still studying the genetics of a large number of these races.

2. *The Melanism of the Nun-moth, Lymantria monacha.*—The nun is one of the moths which have developed melanic varieties within recent times; and these melanic varieties, which were extreme rarities not many decades ago, have almost supplanted the original white form. We have worked out the genetics of this case and shall publish the details when conditions permit. Some of the results were read before the German Zoological Society in 1911 but no abstract was published.

3. *The Genetics of Alpine Varieties, especially of Parasemia plantaginis and the Italian Races of Callimorpha dominula.*—This work has been broken off by the war, but some of the first results are available.

We shall begin with a few facts concerning the geographic variation of the gypsy-moth. We have here a form that is spread all over Europe, through Siberia into China, and all over Japan, infesting, furthermore, part

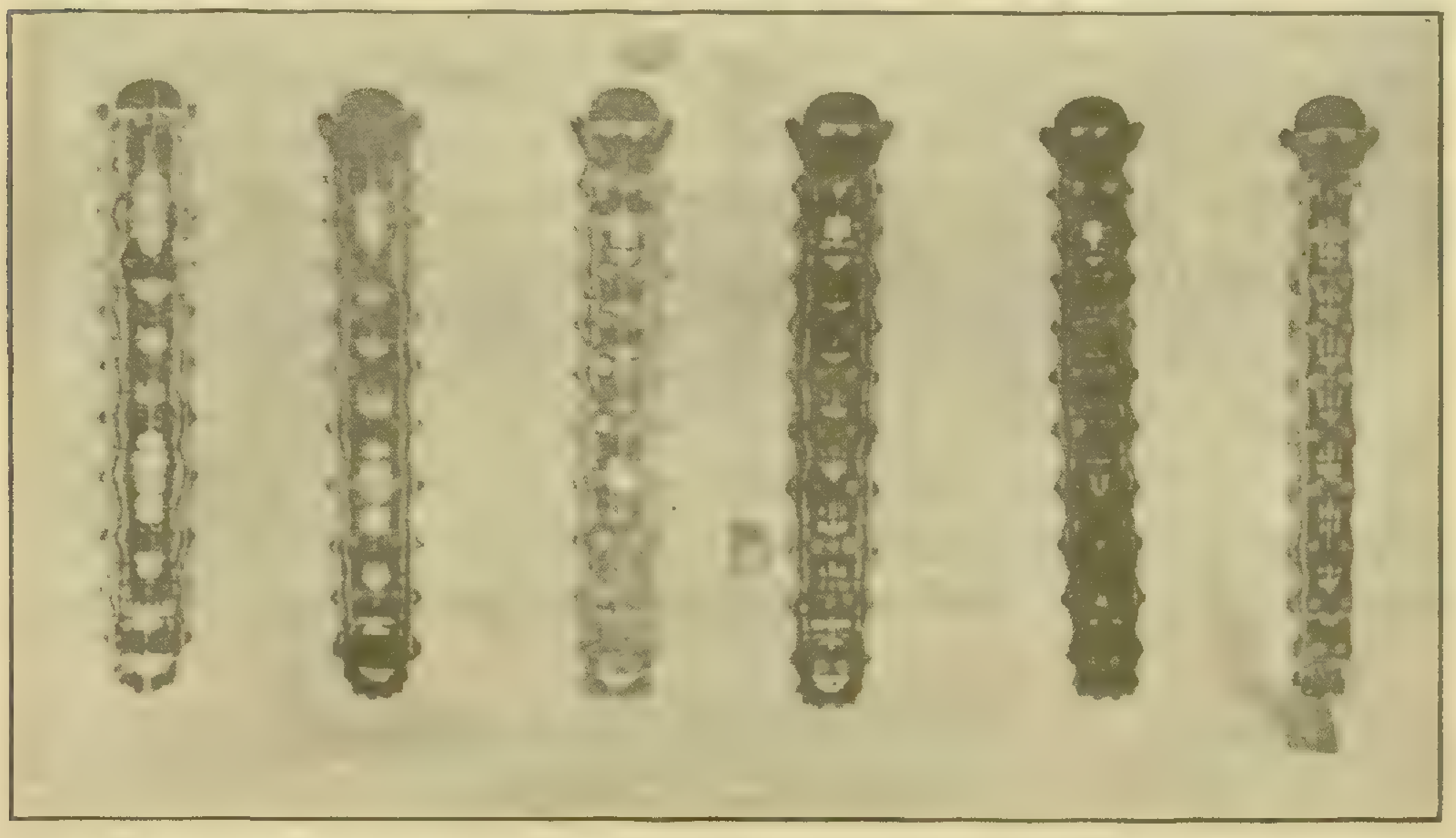

FIG. 1. Types of Caterpillars from different races after the first moult. Drawings by Mr. Yokoyama, Tokyo, 1914.

of the Atlantic coast of the United States. We have studied races from different parts of Europe and Japan and the Massachusetts form and we have found different forms in comparatively near-lying regions. Thus the races from the Rhineland, Silesia and Hungary are dif-

ferent from each other and from the Massachusetts race (probably imported from France). All of them are different from the Japanese races and these again differ in the different parts of Japan. The characters of difference are manifold; we shall confine ourselves here to a single character, more interesting and more characteristic than the others—the markings of the caterpillars. Fig. 1 shows caterpillars of a few races after the first moult. We see here some of the transitional stages from a very light to an almost black caterpillar. The genetic study of this character of marking shows that we are dealing here with a primary type of marking which belongs to the entire group of moths in a similar form, that is, the light pattern. All the darker forms have the same genetic basis of marking, on which, however, dark pigment encroaches increasingly until the markings practically disappear. We may now divide this increasing melanism into ten classes and place the lightest individuals in Class X and the ones without marking in Class I. It must be added that the dark series extends beyond Class I, but the difficulty of classifying them is such that no darker classes have been adopted.

The young caterpillars of the different races show markings which fluctuate around a mean at a certain point of the series and this behavior is remarkably constant for the different races. The following Table I gives a few polygons for different European and Japanese races.

TABLE I

CLASS FREQUENCIES IN PER CENT.

Breed	Race	I	II	III	IV	V	VI	VII	VIII	IX	X
WA3	H	..	..	..	..	..	..	..	38.6	54.5	6.9
UA24	K	..	..	..	..	..	..	15	64.7	20.3	..
UA17	F	..	..	..	..	..	1.5	60	38.5	..	..
VA2	O	..	..	..	..	..	8.2	48.8	31.4	11.6	..
VA8	G	..	..	..	..	..	..	11.8	57	31.2	..
WA4	A	..	..	..	..	19	43	38	..	..	..
WA1a......	S+	..	5.4	19.1	44	30.2	1.3	..	..	..	..
WA56......	M, S	100 (I–III)			..	..	..	..	..	..	..

In crosses of these different types F_1 is about intermediate, as some curves in Table II show.[1]

TABLE II

F_1. CLASS FREQUENCIES IN PER CENT.

Breed	Cross	1	II	III	IV	V	VI	VII	VIII	IX	X
VA17......	S × K	..	..	..	..	17.3	29.6	39.9	13.2	..	..
VA18......	K × S	..	..	..	9.2	33.3	14.4	42.2	0.9	..	..
VA21......	S × A	..	..	..	..	45.4	28.7	25.9	..	..	..
VA22......	A × S	9	20	29	11	15	13	3	..	..	..
VA23......	S × O	..	..	..	4.7	67.4	27.9	..	..	..	..
VA24......	O × S	..	..	..	..	9.9	66.9	22.4	0.8	..	..
VA37......	K × H	..	..	..	..	..	0.7	..	49.6	49	0.7
WA83......	G × M	..	..	2	24	34	32	8	..	..	..
WA88......	M × A	..	..	..	10	70	20	..	..	..	..

And F_2 gives a 1:2:1 ratio, or 3 light + medium : 1 dark, whatever races are involved. (This statement should be taken only on its face value. As a matter of fact, we find here, within the invariably present ratio of 3:1, very strange details of the kind described as "gametic contamination," and, furthermore, an obscuring of the ratio in earlier stages followed later by the right ratio, apparent lack of segregation, etc. From a purely genetic point of view, the analysis of these phenomena constitutes the most interesting part of this work, but it has no special relation to the problems here under discussion.) Back crosses, however, give a 1:1 ratio. The following table gives a few data of this kind.

TABLE III

Breed	F_2 From	Dark, Per Cent.	Light + Medium, Per Cent.
WA12...........	S×K	23.8	76.2
WA13a..........	K×S	25.5	74.5
WA24b..........	S×Ky	25.9	74.1
WA28a..........	A×S	25.3	74.7
WA31...........	O×S	26.2	73.8
WA18...........	S×H	30.2	69.8
ZA20...........	O×M	22.1	77.9
ZA9............	M×H	25.8	74.2
ZA12...........	G×M	25	75

[1] We give here a few random examples. The amount of actual material is very large, as more than 100,000 caterpillars have been bred and studied. We refrain, furthermore, from all such details as behavior in reciprocal crosses, etc.

The actual curves look like the example in Table IV of an F_2 cross.

TABLE IV

ZA9 F_2 FROM M × H

	I	II	III	IV	V	VI	VII	VIII	IX	X
Individuals	24	..	..	..	13	9	29	15	3	..
Per cent	25.8	..	..	..	14	9.7	31.2	16.1	3.2	..

The sum of all the hundreds of curves shows that we are dealing here with a case of multiple allelomorphism: The pigment factor, producing the gradual covering of the markings, is present in the different races in different degrees, all being allelomorphic to each other.

Thus far we have dealt only with the very young caterpillars. Their further history in regard to the effect of these factors leads us one important step further. We find mainly the following types of behavior within the pure races: (1) Light marked caterpillars, which remain practically the same throughout the entire larval life. (2) Light-marked caterpillars which grow darker with every moult and finally are about medium or more than medium dark. (3) Light-marked caterpillars which change during the larval stage, so that they finally are all dark. (4) Medium light caterpillars of different degrees changing to dark during larval life. In the following tables we give a few examples of these races, showing the shifting of the type of marking during the stages of larval life. The large range of variation after the third and fourth moult visible in these tables is due more to a different speed of shifting in different individuals than to the initial variability. This is shown in Table VI, which gives an example of the shifting of types of pigmentation during the larval stages for a series of isolated individuals of some of the pure races.

The genetic analysis of this phenomenon seems to reveal the real nature of the multiple allelomorphs, which cause these different types of pigmentation and their behavior during development of the caterpillars. With-

TABLE V

Examples of Shifting Races

Race H

Class Frequencies in Per Cent.

Stage of Caterpillars	I	II	III	IV	V	VI	VII	VIII	IX	X
3	..	..	..	..	..	..	..	38.6	54.5	6.9
4	..	..	..	..	..	11.8 (VI–VII)		55.3	31.7	1.2
5	29.3	24.4	9.7	12.2	9.8	12.2	.	2.4	..	..
6	64	16	16	4	..	..	..	..	..	..

Race A

Stage of Caterpillars	I	II	III	IV	V	VI	VII	VIII	IX	X
3	..	..	..	..	19	43	38	..	..	..
4	..	..	..	..	35.5	58.1	6.4	..	..	..
5	14.3	42.9	4.7	9.5	28.6	..	..	..	..	..
6	100 (I–III)			..	..	..	..	..	..	..

Race G

Stage of Caterpillars	I	II	III	IV	V	VI	VII	VIII	IX	X
3	..	..	..	..	..	..	11.8	57	31.2	..
4	..	..	..	..	1.4	35.2	33.8	28.2	1.4	..
5	3.6	7.2	14.4	18	25	22.8	9	..	..	..
6	100 (I–III)			..	..	..	..	..	..	..

TABLE VI

Examples of Shifting as observed in Individuals with Different Number of Moults

Race	Individual	Class of the Individual after Moult					
		2	3	4	5	6	Sex
H	ZA3.6	IX	VII	II			♂
"	ZA3.7	VIII	VII	I			♂
"	ZA3.4	IX	III	I			♀
"	ZA3.1	VIII	VII	I	I		♀
A	ZA4.1	VI	V	III			♂
"	ZA4.3	V	III	I			♂
"	ZA4.4	VI	VI	IV	I		♀
"	ZA4.8	VII	V	III	II		♀
"	ZA4.13	VI	V	IV	I		♀
G	ZA6.11	VIII	VIII	VI	II		♂
"	ZA6.7	VIII	VI	VI	IV		♂
"	ZA6.5	VIII	VIII	VI	III		♀
"	ZA6.6	VIII	VIII	IV	III	I	♀
"	ZA6.17	VIII	VI	V	III	I	♀

out going into details, which would necessitate a multitude of tables and curves being given, the following points

are of importance: (1) F_1 between a non-shifting light race and an always dark race is intermediate, or somewhat lighter in the beginning. But by progressive stages the hybrid caterpillars shift over into the dark classes.

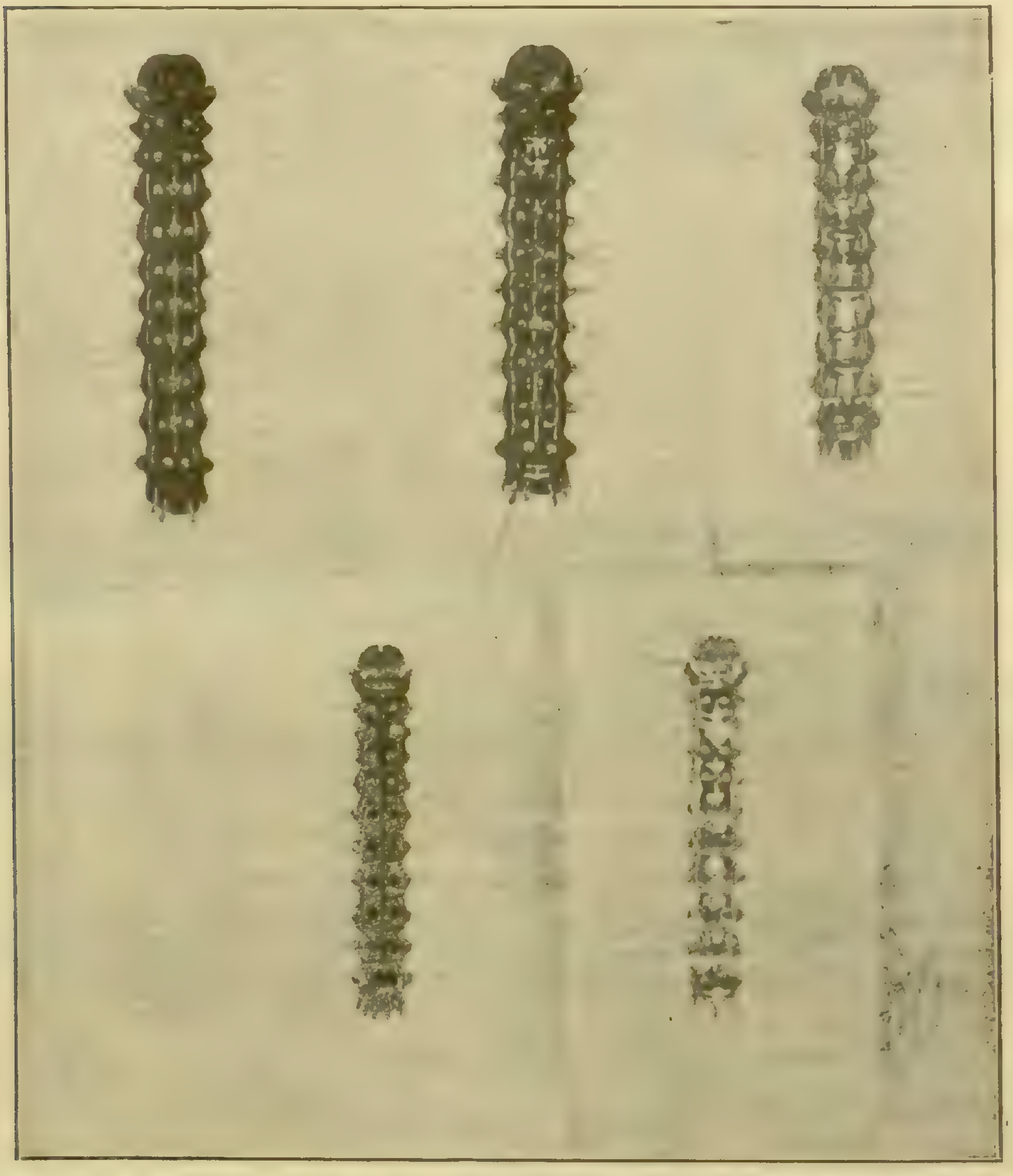

FIG. 2. First row: hybrid between the two parental races after second moult. Second row: Hybrid (left) and light parental race (right) after fourth moult. Drawings by Dr. Poppelbaum, 1912.

Fig. 2 represents caterpillars from a cross of this type. (The exact curves that belong with these pictures are reproduced in our "Einführung in die Vererbungswissenschaft," 2d edition, 1913, p. 170, Fig. 66, as an example

of change in dominance during development.) (2) The same thing happens in certain F_2 crosses, reversing completely during larval life the original ratio of lights and darks. (3) The different races involved are characterized by a difference in the speed of differentiation, as shown in the actual curves. This velocity is also caused by genetic factors. Where these recombine with the pigmentation factors, the entire situation of the F_2 curve is shifted (without changing the 3:1 ratio), showing that the visible effect of the pigmentation factors is bound to a certain velocity of differentiation. (4) The shifting of the type of pigmentation from light to dark during larval life of certain races or hybrids is a process which progresses constantly with time. This is seen when isolated individuals are studied which belong to races that differ in regard to the number of moults and exhibit the shifting simultaneously. There are races where all the male caterpillars have four moults and the females either four or five; other races where the males have four, the females five; others where both sexes have five moults; and in the last case even a sixth moult occasionally occurs. In these cases we see that every new moult produces a further shift to the dark side of the curve, showing that the class of pigmentation to which a full-grown caterpillar belongs is in this case a function of the time of differentiation. The same fact can be demonstrated in a shifting race by prolonging the time between two moults by starvation (which succeeds only to a certain extent). In experiments of this sort it has been possible to get the shifted type of pigmentation, characteristic of the fourth stage, in some individuals in the third stage. Table VI also contains a few random data on the first point. (6) In shifting hybrid cultures there appear comparatively often mosaic-caterpillars, showing different classes of marking on right and left sides. The distance between these two different classes is approximately kept up when shifting occurs during development. The following example demonstrates this fact:

TABLE VII

	Class After Second to Fifth Moult							
	2		3		4		5	
	Right	Left	Right	Left	Right	Left	Right	Left
WA51, 27	IV	III	IV	II	III	I	I	I

These caterpillars always give normal moths and normal offspring.

A careful consideration of these points shows clearly what these multiple allelomorphs for pigmentation really are: They are different quantities of the substance which we call a gene which act according to the mass-law of chemical reactions, *i. e.,* produce a reaction or accelerate it to a velocity in proportion to their quantity. In our special case it means that the factor stands for a metabolic

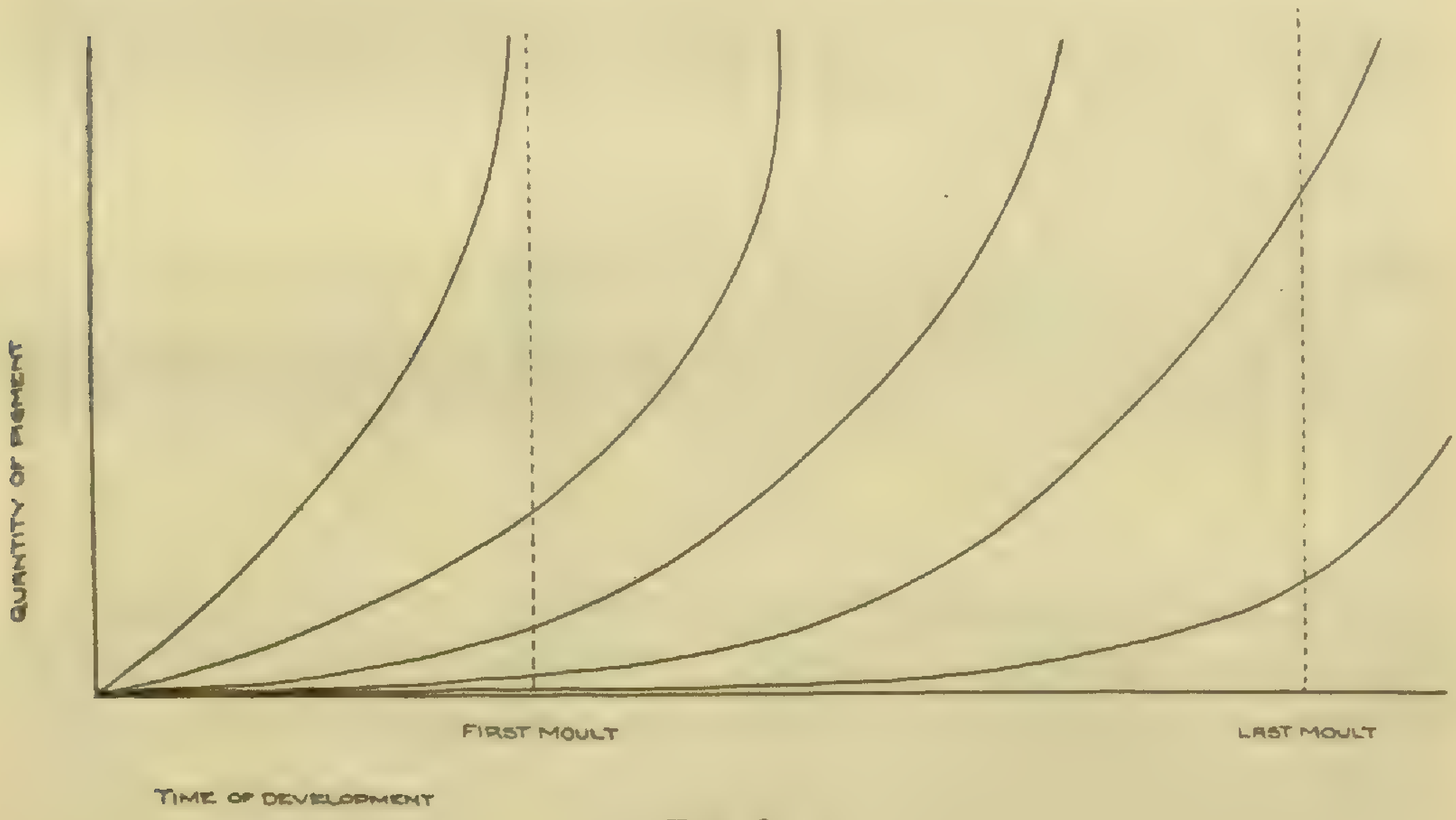

Fig. 3.

activity proceeding with a definite velocity dependent upon the quantity of the factorial substance present. This activity finds its visible expression in the deposition in the skin of increasing quantities of certain products of protein decomposition which as chromogens are oxidized into melanin pigments. The effect of the different quantities of active substance (enzyme?) which we call the multiple allelomorphs upon the progressive pigmentation

of the caterpillars is then represented by the graph on p. 36 (Fig. 3).

Given a definite quantity of the factorial substance and identical conditions, the velocity of the reaction is constant. Thus the final result depends upon the amount of the factorial substance present and the independently inherited rapidity of differentiation, which determines the situation of the growth-stages on the abscissa (the dotted lines). Thus the above quoted facts as well as the multitude of details not mentioned can be easily derived from this graph. The last named mosaics are of course the expression of small differences in the velocity of differentiation in symmetric halves of the body, which are well known to embryologists.

These conclusions in regard to the real character of multiple allelomorphs are the same as those derived from other characters in the same objects. In our work on intersexuality we were able to prove, to as great an extent as a genetic proof can possibly be carried, that the different geographic races of the same moth differ in regard to the absolute and relative quantities of the substances, which we call the sex-factors. In the genetic language of the present day we should call them, therefore, multiple sex-allelomorphs, a conception which indeed we have always used (without this recent term) since our first report about this work in 1911. In the case of intersexuality we can furnish facts very similar to those about the caterpillars, if we consider certain features of the wing colors. In normal males a certain amount of pigment covers the entire wing, whereas the female wing is unpigmented. This pigment is formed by the oxidation of a chromogen deposited within the scales. There it flows from the wing veins with the blood. By a detailed analysis we are able to show that an intersexual male is a genetic male which developed as such up to a certain point when the development suddenly began to continue under the aspects of femaleness. One of the results of male metabolism is the production of these chromogens

in late larval stages. This production is therefore stopped when female metabolism sets in; when then the time arrives in development, when the chromogen spreads over the wing scales, its available amount is proportional to the relative lateness of the reversal of sex. Therefore, with increasing intersexuality, the pigment flowing from the veins covers a smaller and smaller area of the wing, finally being confined to the neighborhood of the veins. As[2] the analysis of the other intersexual organs allows an accurate determination of the time factor involved, we have here a very close physiological parallel to the facts about the caterpillars.

In most other cases of multiple allelomorphism only the results can be seen, and it will be difficult to work out the time factor, which proves that the multiple allelomorphs are different quantities of an active substance. (Some botanical subjects ought, however, to be favorable.) But in comparing the other facts about multiple allelomorphs with our cases, we feel confident that, whereever a similar analysis can be applied, the results will be the same. For example, all the cases of quantitatively different pigmentation, which are of multiple allelomorphic nature, like Castle's hooded rats or our different cases of melanism in moths, show that the effect of the different factors is that different quantities of pigment spread from different "points of outlet," which of course are hereditary traits of the species or group; the similar effect, therefore, leads to suspect a similar cause.

If our conclusions regarding the nature of multiple allelomorphs are accepted, it must lead to a different intellectual attitude toward the problem of variability of genes, which is so important for evolution. The opposition to the view has been, we believe, primarily on aprioristic grounds. In the long controversies of recent years regarding the interpretation of Castle's work the logical side of the case seems to have always been in the foreground. The same is the case when E. Baur calls our

[2] See pictures in *Jour. Exp. Zool.*, 22, 1917, pp. 614–15.

views in regard to the variability of the sex-factors *a priori* inadmissible. We believe that this intellectual attitude toward the problem is the result of Johannsen's doctrine of agnosticism in regard to the nature of the gene, which resulted in a kind of mystic reverence, abhorring the idea of earthly attributes for a gene. (Our distinguished opponents will excuse this somewhat extreme statement.) If, however, it can be proven that genes are substances with the attribute of definite mass, it would be illogical to deny their variability. Nobody will claim that a gene is a substance that passes unaltered from generation to generation. The elementary facts of development and regeneration show that this substance grows, at least, and increases in quantity. If, now, the substantial basis of heredity in the sex-cells is established by the assembling of all the factor-substances in their characteristic quality *and their correct quantity,* the situation is the same for the gene as for any other organic process: the varying conditions of the surroundings of the gene cause a certain amount of fluctuation in its quantity. This conclusion entirely changes the logical aspect of the question, whether or not a change of the gene by selection of variants is possible.

The strongest point of the anti-selectionists was that it is absurd to assume that a selection of somatic fluctuation has anything to do with the characters of the germ-plasm. With the quantitative view, however, which we believe to have proven in two elaborate cases, this situation changes. The somatic character in question, say amount of pigmentation, can only change toward a plus or minus side. This change is caused directly by a difference in the velocity of the reaction of some metabolic process which results in the deposition of pigment. Such a change of velocity of reaction, however, can be produced either by the action of the medium, and then it is a modification, or by fluctuation in the quantity of the gene, causing increase or decrease in the velocity. The resulting variation is of course, phenotypically, the same. Selection, therefore,

may be ineffective, if a modification only is selected; it will be partly successful if a combination of plus-quantity with plus-modification is selected; and fully successful if the exclusive result of plus-quantity of the gene is selected. The *deus ex machina* modifying factor, which, moreover, does not fit the decisive genetic facts in the most discussed case of Castle's rats nor our cases, thus becomes superfluous.

It is, moreover, perfectly logical to assume that selection of either plus or minus quantities of the genes changes the mode of the fluctuation of this quantity correspondingly in the succeeding generation. If the different quantities of the substances, which constitute the systems of multiple allelomorphs, are inherited, then every other quantity is also inherited. If the presence of the quantity p in the germ cells of the parents causes the reappearance of the quantity p in the germ cells of the children, the same fact applies to the quantities q, r, s—to every quantity which is present or has been selected. Selection can, therefore, change the quantity of the gene, and also, therefore, the somatic characters caused by quantitative differences in the gene, until the physiological limit is reached. This limit may be the limit for the character in question—for example, no pigment, self-color—or it may be the limit set by the necessary coordination of developmental processes. For example, in the development of a moth a certain gene causes, at a certain moment—during pupation—the evagination of the imaginal disks of the antenna. The correct quantity of the gene causes this process to take place at the correct time. A quantitative variation of the gene would cause the evagination to take place at the wrong time. We have, indeed, had strains of caterpillars where in many individuals this process took place in the last stage of the caterpillar, giving caterpillars with pupal antennæ. The quantity of the gene in question was in these cases not coordinated with the other genes and the action was produced too early. It is evident that quantitative changes

of this kind will lead to physiological impossibilities, monsters, etc. Here, then, is again the limit for selection of factorial quantities. It need hardly be added that such selection is necessarily orthogenetic.

Our own experiments in this line are, as far as they go at present, in perfect accord with Castle's work. We have, moreover, applied another type of experimental test, namely, selection in F_1. If a given pair of multiple allelomorphs differs in regard to the quantity of the factorial substance and this quantity is subject to fluctuation around a mean, the variability of the character in F_1 is caused by the usual agencies producing fluctuations as well as by the different combinations of the parental quantitative values. Selection in F_1 ought, therefore, to influence the curve in F_2 in a certain number of cases, namely, when the plus or minus individuals are genetically plus or minus. Within the normal segregation of light and dark individuals in the 3:1 ratio a shifting of the mean for lightness and darkness must take place. In a series of such experiments we had a number of positive results. The following Table VIII may serve as an example:

TABLE VIII

F_2 WITH SELECTION IN F_1 FROM CROSS K × S

	In Third Stage									
	I	II	III	IV	V	VI	VII	VIII	IX	X
Plus selection	25.5	..	..	7.3	12.7	9.1	30	15.4	..	..
Minus selection	25	5.7	26.9	15.5	17.2	3.2	6.5	..	..	..

We believe that these facts and interpretations have a definite bearing on the problem of evolution. The first step in the differentiation of species which occurs in nature seems to be the formation of geographic races. The entire bulk of modern evidence in ecology tends to show the existence of clearly defined local forms for very restricted areas. For example, the ichthyologists differentiate forms of Salmonids and Coregonids for practically every river and lake; in the same way in the lower

organisms, like Daphnids and Rotatoria, different forms appear in different regions. The ornithologists describe different races for every river basin of the affluents of the Amazonas; the mammalogists do exactly the same thing for every area which was thoroughly covered. Where breeding experiments have been carried on it has been shown that the geographic races may be perfectly fertile with each other and may produce fertile offspring. In some cases, however, the transitional stages toward sterility are found. Thus the production of intersexual moths in crossing geographic races can be regarded as a step toward increasing incompatibility, which in one of the crosses attempted by us was an absolute one. In other cases only a small percentage of the offspring of the hybrids could be reared, as in the crosses of the North and South European *Callimorpha dominula*. We, therefore, with many evolutionists, feel convinced that the geographic races are the most important visible steps in species-formation in nature.

If we now look into the characters distinguishing geographic races, we very often find certain qualitative differences most conspicuous, for example, exchange of red and yellow color in the moths. A close study of definite examples, however, reveals that these differences are often more conspicuous than important. This is shown by the only group of information in the animal kingdom which we have both by ecological and genetic work—the geographic variation of land snails. The facts about the extreme variability of *Helix, Achatinella, Partula*, etc., are well known, as well as the irregularities in the confinement of definite types to definite localities. We have been so fortunate as to gain some insight into these facts through a very interesting collection which Dr. Haniel made in Timor and studied under our direction (not yet published). It was evident here, as in the other cases, that a series of unit factors for number, color, form of bands and ground color, which recombined freely, was involved. And practically all the combinations could be

reduced to the genetic factors which Lang worked out for *Helix*. But, exactly as in the classic cases, there was no possibility of stating a definite relation of these factors to the grouping according to localities. In some localities certain factors or combinations did not occur, but the attempt to classify the material along this line proved a failure. However, every group from each locality exhibited beside these factorial recombinations certain quantitative characteristics of size, proportions, etc., of the shell which were characteristic for definite localities. These, however, are the characters which probably fall in line with those caused by the quantity of the genes.

The difficulties which the facts of geographic variation create for the conception of species-formation by selection have often been discussed. Bateson in particular ("Problems of Genetics") scrutinizes them from the modern genetic point of view. They are indeed insuperable if all characters which show variations and recombinations are considered from this point of view. The extreme irregularity, for example, of the local combinations of types of shells in *Helix, Partula* and *Achatinella* makes it impossible to regard them as local adaptations. This is certainly true, but may be without any bearing on the species question at all. The factors and recombinations occurring in *Helix, Achatinella* and *Prodromus* are more or less the same, just as are the recombinations of coat colors in different rodents. They constitute a set of mutations and their recombinations which are proper to the type of germ-plasm of the group. They occur, recombine or fail to appear as chance wills, and seem to have no special selective value. We do not think that these are the characters which play a part in the evolution of species; they are, in most cases, independent of adaptation.

There are, however, reasons for supposing that such differences of characters as are based on the quantitative differences of the gene are those which are influenced by selection and are important for the formation of the first

steps toward diversification of species. We base this opinion on the following facts:

One of the few cases where selection in nature has apparently been seen at work under our eyes is the much-quoted case of melanic moths. We started in 1908 to work out the case of the nun, *Lymantria monacha*. The dark varieties of this moth have been known as rare occurrences for over a century. But only during the last decades have they spread and almost replaced the white forms. The analysis of the genetics of this case shows that the dark form is a dominant mutation to the white and that the many different stages of darkness, which form a complete series from white to black, are produced by sex-linked multiple allelomorphs. (Unfortunately, the interesting details can not be given at present.) How is it, now, that these combinations have come to replace the original form? Many hypotheses, some of them very strange, have been put forward; but it seems to us that the case is comparatively simple. The dark forms are stronger, more lively, better fliers, as far as we can tell from our experience with the animals in captivity. They are also larger (see Fig. 102, p. 267, in our "Einführung in die Vererbungswissenschaft," 2d ed., 1913). The melanism is in this case, therefore, only the most conspicuous superficial feature of a quantitative and progressive change in a gene which causes a definite metabolic condition, resulting in hardiness as well as in the deposition of more pigment in the wings. The quantitative change has here a superficial expression and is therefore easily recognizable. But this visible pigmentation is not the really important character. How is it, then, that these melanic forms, and other forms in similar manner, have established themselves so suddenly? We may venture to point to the facts that the selection, as has often been stated, has occurred especially near the larger cities, and that the period during which this selection has taken place is the period of industrial development, *i. e.*, of restriction of forested areas near the cities. It is,

furthermore, the period of scientific and intense forestry and of economic entomology. Here we have the probable agencies that made life difficult for the moth and gave a great selective value to that advance in hardiness which lies behind the melanic appearance.

We should point out here the difficulties which arise in the criticism of definite views of evolution on the basis of facts not analyzed genetically. The selective value of a climatic character may often be doubted on the ground that the same type occurs in a very different area admixed with the local form. But genetic analysis may often show that what appears to be the same type is in reality a different thing. The north European Arctiid, *Callimorpha dominula*, has wings marked with red; the Italian form has wings marked with yellow. In certain localities (one of them near Berlin) a yellow sport of the red form regularly appears, apparently the same form as the Italian one. We, as well as others, have crossed these forms. The yellow sport is a simple recessive to red and segregation occurs in the 3:1 ratio. The Italian yellow form, however—at least the ones from the Abruzzi, which we used—crossed with the red northern form, produces intermediate orange in F_1 and in F_2 every shade from red to yellow. The two yellows, which look alike and probably are chemically alike, are nevertheless products of a different metabolic process. In the sport the same metabolic process which usually leads to red pigment is changed by mutation only to the extent of the color change in the end-product. In the southern form a different type of metabolism results in the formation of yellow pigment, and the cross is therefore an entirely different cross, with different results.[3] As a matter of fact, the latter cross shows very much diminished fertility, as Standfuss has already pointed out. This shows how unsafe the ground is on which criticism of evolutionary questions without genetic test is based. That our example is not an exception is proved by the fact that Standfuss long ago formu-

[3] We may point out that herefrom a rational interpretation of dominance and blending can be derived.

lated the rule, that when two forms coexist in the same locality and are able to interbreed, they do not produce intermediates; but when the forms are geographically separated as local races, crosses between them result in a series of intermediates. Bateson says: "In this aphorism there is a good deal of truth." We think that the rule expresses the difference between a non-adaptational chance mutation and the adaptational change in the factorial quantities which may lead to a similar-looking, but physiologically different character. This character, although, like the non-adaptational one, is itself of no selective value, is the result of a general physiological change which does have a selective value.

This will become still more evident if we return once more to the study of the gypsy-moth. In studying the relations of the different geographic races as characterized by the multiple-allelomorphic characters in question, we find that these characters are paralleled closely by differences in the life-cycles. Without going into details, we may state as a fairly general rule that the races with high degrees of pigmentation in the later stages are the ones which show a fast development, comparatively short larval life and a long period of hibernation. The light races have a comparatively long larval period and a correspondingly short period of hibernation. The former races, furthermore, inhabit the areas where a long and cold winter occurs, while the latter are endemic in places which have a hot summer, early spring and mild winter. One might think that these different characteristics were simply the direct effect of temperature conditions. But that this is not the case is shown by the constancy of the differences when the races are bred in a different climate and also by experiments on the physiology of hibernation, which have convinced us that the time relations of the life-cycle are—of course, within the limits of fluctuation—a heritable trait of rhythmic character. These facts show where the adaptational character of the differences of the geographic races lies: the adaptation which fits the differ-

ent milieus is the life-cycle (in a broad sense). The visible distinctive characters of the races—aside from additional mutations of a non-selective nature—are nothing but the products of reaction of different types of metabolism, allied with the different time relations of the cycle. The method of the formation of geographic races in this case must, therefore, be the following. The first conquest of a new territory is of course only possible when the animal is preadapted, along general lines, to the new medium. But that it can maintain itself depends upon its power of special adaptation. The gypsy-moth, for example, has repeatedly been brought into England, but it has never established itself there. In the case of this form the special adaptation means the coincidence, in the first place, of the life-cycle with the seasonal cycle in nature. And it is here that all the discriminating effect of selection comes in. The quantitative changes of the genes which cause the time relations of the cycle are then the material for selection, and selection acts according to Darwinian principles until the equilibrium is established. Thus the genetic study of the quantitative changes of the gene reveals anew the truth of Darwin's conception. Furthermore, we see here how sterility of hybrids or complete incompatibility of new forms may arise. We have proved that the quantitative differences of the sex-factors, which are themselves nothing but adaptations to the time-relations of the cycle, are among the characteristic differences of these races.[4] There are, moreover, responsible for the incompatibility in regard to sex which results in intersexuality after crossing. Changes of exactly the same type may easily make any cross-breeding impossible, since no organism can develop unless all the processes of differentiation are coordinated in respect to their velocity. Here we see, finally, why geographical races are so often uniform and are characterized by certain traits of

[4] Compare also Pflüger's and R. Hertwig's work with frogs and Cuénot's with starfish, demonstrating similar facts in regard to geographic variation of sexuality.

a quantitative character even when additional mutations and their recombinations make them at first sight appear diversified. This uniformity indicates the adaptational type produced by selection of the quantitative variations of some vital gene; the differences are only a difference in apparel.

In conclusion, we may point out three groups of facts which, of the greatest importance for evolution, have always been a hard nut for the mutationists to crack. The first is the series of temperature-experiments in Lepidoptera—and similar experiments in Amphibia, Crustacea, etc.—that lead to the production of aberrant forms which resemble closely certain geographic varieties. But, with the exception of certain often-quoted cases, these aberrations are not hereditary. In the light of our experiments these facts are not surprising. The effect of the temperature experiments is to change the normal time-curve of certain metabolic processes. The effect is, therefore, due to this change of one of the variables of the reactions in question. The quantitative change of the substance of a gene, however, which we found to be at the basis of the geographical variations, also produces a difference in respect to the time-curve and therefore the same effect, this time a heritable effect. If we now select the plus individuals in this type of experiment—and this applies to all analogous experiments—we may simply select a modification. But we also may select the combination of a plus-modification with a plus quantity of the gene in question. If the experiment is repeated, the next generation will then show a still stronger reaction, or, if the experimental influence is not repeated, there will be an after effect of the experiment on the parents. It is remarkable that such results, which were to have proved the inheritance of acquired characters, always turned out, when characters relating generally to the life-cycle were in question, characters which also appear in the geographic races of the form. Extreme mutationists used to deny or disregard these facts. Here we have a simple

explanation for them which both does justice to the facts themselves and falls in line with modern genetic views.

Furthermore, we now see the exact meaning of Darwin's view, which he had to express in a somewhat ambiguous way on account of the lack of experimental data which would have permitted clearer expression. His essay of 1842, the forerunner of the "Origin of Species," begins with the words: "An individual organism placed under new conditions sometimes varies in a small degree and in very trifling respects, such as stature, fatness, sometimes color, health, habits in animals and probably disposition. . . . Most of these slight variations tend to become hereditary." This statement shows clearly what Darwin had in mind. If he assumes that some variations, which are produced by change of conditions, are sometimes non-heritable, but tend to be inherited, we can now explain what this means. The variations which, as geographic races, form the first steps in the formation of new species are indeed exactly the same whether or not they are inherited. Their direct physiological cause is also identical, being a change in the rate of a definite process during differentiation. Only the ultimate cause is different; in the one case the original quantity of the gene determines the rate of differentiation—which then is hereditary—from the beginning; in the other case an outside factor is active, retards or accelerates the same reaction to the same degree. With this additional bit of interpretation, Darwin is right, after all.

The other group of facts includes certain details of mimicry (mimetism). We believe that the general principle of mimetism has been fully explained genetically by Punnett. But there are certain details which his selectionist opponents point out which constitute strong evidence against Punnett's view. We think that the most valid argument against the Mendelian view of mimetism has been derived from the facts about the parallel geographic variation of model and mimic. If our genetic conception of geographic variation is correct, this point

is not difficult to understand. If the resemblance of model and mimic is based on the presence of similar chance- or non-chance combinations of genetic factors, and if geographic variation consists in the specific adaptation of the quantity of certain genes to a required velocity of some vital reaction, it is very natural that similar genes in model and mimic should be in exactly the same situation and should undergo parallel changes.

The third important set of facts to be considered is the problem of domestication. Darwin's view is well known, as well as the solution of a great part of the problem through Mendelism. The latter shows that selection of the recombinations after cross-breeding (besides picking of mutations) is the chief source of success in domestication. (See our demonstration of this fact regarding the improvement of pigs in "Einführung in die Vererbungswissenschaft," 2d ed., 1913, pp. 276–80.) That this fact was well known to Darwin is shown, for example, in his report about Lord Orford's greyhounds ("Variation of Animals," etc., Ch. 1). But he believed, in addition, in a positive effect of selection of small variations. Wherever he tabulates such characters, most or all of them are quantitative characters of a kind which we can assume to be dependent upon the presence of definite quantities of a gene. Here we may have the solution of the difficulties which the problem of domestication affords in spite of mutation and recombination. No doubt the high capacity for fattening was crossed into our hogs with Asiatic forms. But selection of plus-quantities of the responsible gene enabled us to obtain the character as it stands to-day.

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MATERNAL INHERITANCE IN THE SOY BEAN

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THE soy bean, *Glycine hispida* Maxim., shows as different types two cotyledon colors, yellow and green. The beans with yellow cotyledons have two types of seed-coat colors, namely, green and yellow, while the beans with green cotyledons have always green seed-coats.[1] The inheritance of these types of cotyledons and of seed-coats has been proved by the author's experiments to be maternal. A brief notice of the experiments will be given in the following.

The green and yellow colors of cotyledons and seed-coats are obviously attributed to chlorophyll, which, on the ripening of the beans, is either changed from green into yellow or remains green. Further, according to the author's observations, the chlorophyll in the vegetative parts of the plant shows the same behavior as the chlorophyll of the cotyledons; in other words, the leaves and stems of the varieties with yellow cotyledons turn to a yellow color when they are gradually dying coincident with the ripening of the beans, while those of the varieties with green cotyledons remain green sometime after the dying of the whole plant. These facts suggest that the two types of cotyledon colors may represent two kinds of chlorophyll, one which changes into yellow under certain physiological conditions and one which is not so affected. The chlorophyll of the seed-coats, however, seems to behave somewhat differently from the chlorophyll in all

[1] Black and brown pigments also appear in the seed-coats of certain varieties. These pigments are entirely independent of the green and yellow colors here referred to in their inheritance, but they make the latter colors invisible or at least indistinct. By proper crosses, however, one can test whether a seed-coat covered by the black or brown pigment belongs to the green or the yellow category.

TABLE I

SOY BEAN CROSSES MADE IN STUDYING THE INHERITANCE OF GREEN AND YELLOW COLORS OF COTYLEDONS AND OF SEED-COATS

	Crossing No. I		Crossing No. II		Crossing No. III		Crossing No. IV		Crossing No. V		Crossing No. VI	
	Cotyledons	Seed-coat	Cotyledons	Seed-coat	Cotyledons	Seed-coat	Cotyledons	Seed-coat	Cotyledons	Seed-coat	Cotyledons	Seed-coat
Parents												
Female	green	green	green	green	yellow	yellow	yellow	green	yellow	yellow	yellow	green
Male	yellow	yellow	yellow	green	green	green	green	green	yellow	green	yellow	yellow
F_1-Ind.	green	green	green	green	yellow	green	yellow	green	yellow	green	yellow	green
No. Ind.	24	24	3	3	40	40	4	4	9	9	5	5
F_2-Ind.	green	green	green	green	yellow	green yellow	yellow	green	yellow	green yellow	yellow	green yellow
No. Ind.	3,129	1,248	322	216	11,836	825 : 288	846	436	1,815	418 : 128	169	56 : 19
						(74.1% : 25.9%)				(76.6% : 23.4%)		(74.7% : 25.3%)
F_3-Fam.	green-constant		green-constant		yellow-constant		yellow-constant		yellow-constant		yellow-constant	
No. Fam.	1,248		216		1,113		436		546		74	
No. Ind.	72,501		16,498		28,231		2,341		55,354		4,635	

other parts of the plant, since, as was already noted, yellow cotyledons are accompanied by green seed-coats in certain varieties.

The crossing experiments which have been made by the author since 1910 with these different types of beans have produced the results shown in Table I, the main facts being summarized as follows.

I. The F_1 cotyledons of the crosses reciprocal to each other are of the same character as the female parents. In respect to the cotyledon colors, the F_2 and following generations show the characters of the F_1 generation exclusively, instead of a Mendelian segregation between the yellow and green colors. Hence we are probably dealing with characters which can be inherited only through the female parents.

II. The inheritance of the seed-coat colors is a more complicated phenomenon. In the cross "green cotyledons, green seed-coat" (♀) × "yellow cotyledons, yellow seed-coat" (♂), the green seed-coat is inherited through the female parent exclusively, just as in the case of the cotyledon colors; but in the reciprocal cross the green and yellow seed-coats show Mendelian segregation, the former being dominant.

The maternal inheritance observed above was not due to self-fertilization succeeding failures in artificial crossing, because several other characters showed inheritance through the male parents.

An interpretation of the inheritance phenomena under consideration is suggested as follows. In the first place, let us refer again to the two different kinds of chlorophyll assumed to be concerned in producing the green and yellow cotyledons; namely, the chlorophyll which can be changed into yellow and the chlorophyll which remains green. (These will be denoted respectively as "(Y)" and "(G)" in the later descriptions.) These characteristics of chlorophyll may be due to heritable traits of the chromatophores or of the cytoplasm, and not to hereditary elements in the nucleus. As, on the fertilization of

the egg-cell, the chromatophores and the cytoplasm of the female gamete will probably remain as such without being supplemented by those from the male gamete, their characteristics would naturally be inherited only through the female parent. In the second place we may assume that a pair of Mendelian factors is concerned in the inheritance of the colors of the seed-coats. The factor "H" inhibits the chlorophyll "(Y)" in the seed-coat of the beans with yellow cotyledons from changing to yellow, producing beans with yellow cotyledons and green seed-coat; the absence of the factor "H," expressed by "h," allows the seed-coat of the bean with yellow cotyledons to remain yellow. The seed-coat of the bean with green cotyledons remains green no matter whether the factor "H" is present or absent, because the beans of this kind have the chlorophyll "(G)" which is incapable of changing the color.

The justice of the contention regarding the bean with green cotyledons, moreover, is supported by the following observations. The F_2 families of the crosses "green cotyledons, green seed-coat" (♀) × "yellow cotyledons, yellow seed-coat" (♂) were actually composed of two kinds of individuals which were distinguishable from each other by a slight difference of the intensity of green color in the seed-coats, and the numerical relation between these two kinds of individuals was approximately the Mendelian mono-hybridal segregation ratio, the darker seed-coat being dominant to the lighter one. Again, in the F_3 generation of these crosses, there were obtained three types of families, two which were uniformly of the darker and of the lighter seed-coats respectively and one which was a mixture of both. By comparing the green seed-coats of the female parents in these crosses with those of the progeny, the former was found to belong to the darker class mentioned above. These variations in the green color of the seed-coats may be regarded as being due to the influence of the Mendelian factors "H" and "h" respectively on the chlorophyll "(G)"; from which it follows

that the method of inheritance in the beans with yellow cotyledons obtains also in the beans with green cotyledons.

Keeping these statements in mind the cases in Table I may be illustrated as follows:

	Crossing No. I	Crossing No. II
Parents	(G)HH (♀)×(Y)hh (♂)	(G)HH (♀)×(Y)HH (♂)
Cotyledons	green yellow	green yellow
Seed-coat	green yellow	green green
F_1	(G)Hh	(G)HH
Cotyledons	green	green
Seed-coat	green	green
F_2	(G)HH (G)Hh (G)hh	(G)HH
	25% 50% 25%	100%
Cotyledons	green	green
Seed-coat	green	green

	Crossing No. III	Crossing No. IV
Parents	Y(hh) (♀)×(G)HH (♂)	Y(HH) (♀)×(G)HH (♂)
Cotyledons	yellow green	yellow green
Seed-coat	yellow green	green green
F_1	Y(Hh)	Y(HH)
Cotyledons	yellow	yellow
Seed-coat	green	green
F_2	(Y)HH (Y)Hh (Y)hh	(Y)HH
	25% 75% 25%	100%
Cotyledons	yellow yellow	yellow
Seed-coat	green yellow	green

If the foregoing interpretation really represents the facts in this investigation, we may consider also crosses in which forms such as (G)Hh, (G)hh, and (Y)Hh were used as the parents, since in these crossings phenomena different from those in Table I would be expected. These expectations have been fulfilled in further experiments in which individuals from the previous experiments representing different intensities of seed-coat color were used as the parent plants. The results of these crosses, accompanied by interpretations, are shown in Table II.

TABLE II

CROSSES MADE AMONG THE PROGENY OF THE HYBRIDS SHOWN IN TABLE I

		Parents		F1		F2	
		Female	Male	Character	No. of Individuals	Character	No. of Individuals
Crossing No. VII	Cotyledons	yellow	green	yellow	22	yellow	2,381
	Seed-coat	yellow	green	yellow	22		
	Interpret.	(Y) hh	(G) hh	(Y) hh	100%		
Crossing No. VIII	Cotyledons	yellow	green	yellow	18	yellow	1,963
	Seed-coat	green	green	green	10		
				yellow	8		
	Interpret.	(Y) Hh	(G) hh	(Y) Hh	50%		
				(Y) hh	50%		
Crossing No. IX	Cotyledons	yellow	green	yellow	9	yellow	1,108
	Seed-coat	green	green	green	7		
				yellow	2		
	Interpret.	(Y) Hh	(G) Hh	(Y) HH	25%		
				(Y) Hh	50%		
				(Y) hh	25%		

The maternal inheritance described in this paper seems to be essentially the same phenomenon as the inheritance of the character "*albo-maculata*" which was studied by Correns[2] in *Mirabilis Jalapa* and also by Baur[3] in *Antirrhinum majus*. In each case one is dealing with chromatophore characters.

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[2] Correns, C., *Zeitschr. f. ind. Abst. u. Vererbungslehre*, Bd. I, 1909, pp. 291–329; *Ibid.*, Bd. II, 1909, pp. 331–340.

[3] Baur, E., *Zeitschr. f. ind. Abst. u. Vererbungslehre*, Bd. IV, 1910, pp. 81–102.

SHORTER ARTICLES AND DISCUSSION

LINKAGE IN MAIZE: THE *C* ALEURONE FACTOR AND WAXY ENDOSPERM[1]

In 1912 Collins[2] presented data which showed a linkage between waxy endosperm and aleurone color in certain hybrids of Chinese and American corn. A summary of the F_2 data in Table II, p. 579,[2] gives the coefficient of association as .821. This is equivalent, approximately, to a 3.5–1 gametic ratio, and a crossing-over percentage of 22. The percentage of waxy grains is about 21 and colorless about 25. This is good evidence that Collins is dealing with material heterozygous for waxy endosperm and heterozygous for only one factor in aleurone. In the back cross data in Collins's Table IV none of the ears shows the 1:1 relation between colored and colorless expected from plants heterozygous for one color factor. The material in that table apparently involves more than one aleurone factor in the heterozygous condition and before such data may be considered in any linkage study they must be corrected for this or the true values for the percentage of crossing over can not be ascertained. The coefficient of association need not be used if we are dealing with back cross data. If it seems desirable to use the coefficient of association with this sort of data new tables should be calculated from the gametic series $n:1:1:n$ corrected for the respective aleurone factor conditions.

The advantage of back cross data is obvious. Data of this nature obtained by the writer from crosses of plants heterozygous for one aleurone factor and for waxiness with double recessive plants are presented in the table on p. 58.

Families 6, 99, and 100 are derived from colored corneous seeds heterozygous for aleurone and waxiness. Families 9 and 101 are colorless waxy plants. The first nine ears give an average crossing over of 26.7 per cent. or a gametic ratio of 2.75:1. Ears 8 and 9 show repulsion instead of coupling, but this does not

[1] Paper No. 66, Department of Plant Breeding, Cornell University, Ithaca, N. Y.

[2] "Gametic Coupling as a Cause of Correlations," AMER. NAT., 46, pp. 569–590. 1912.

necessitate a separate summary for the crossover and non-crossover classes of the coupling and repulsion families. The deviations from the average are more than twice the probable error in ears 1, 3, 4, and 9, between one and two times in ears 5 and 7, and less than the probable error in ears 2, 6, and 8.

BACK CROSS DATA: HETEROZYGOUS CORNEOUS COLORED × WAXY COLORLESS

Ear Number	Parentage	Corneous Colored	Corneous Colorless	Waxy Colored	Waxy Colorless	Non Cross-overs to Cross-overs	Per Cent. of Crossing Over	Deviation from 26.7 Per Cent.	Probable Error in Per Cent.	Dev./P.D.	Per Cent. Waxy	Per Cent. Colorless
1	100(6)×101(1)	147	58	65	133	280:123	30.5	3.8	1.49	2.55	49.1	47.4
2	100(1)×101(3)	104	24	32	67	171: 56	24.7	2.0	1.98	1.01	43.6	40.1
3	101(9)×100(9)	102	60	43	137	239:103	30.1	3.4	1.61	2.11	52.6	57.6
4	100(5)×101(4)	170	49	39	136	306: 88	22.3	4.4	1.50	2.93	44.4	47.0
5	101(3)×100(8)	124	53	60	153	277:113	29.0	2.3	1.51	1.52	54.6	52.8
6	101(5)×100(6)	71	24	9	31	102: 33	24.4	2.3	2.57	.89	29.6	40.7
7	100(11)×101(4)	140	42	63	124	264:105	28.5	1.8	1.55	1.16	50.7	45.0
8	101 (2)× 99(1)	46	111	103	32	214: 78	26.7	0	1.75	.00	46.2	49.0
9	99 (1)×101(9)	69	229	195	60	424:129	23.3	3.4	1.27	2.68	46.1	52.3
	Total					2,277:828	26.7		0.54		47.7	48.4
	6 (6)× 9(6)	118	114	128	131	249:242	49.3	22.6	1.35	16.74	52.7	49.9

Owing, perhaps, to the difficulty in separating waxy from corneous grains the percentage of waxy grains for the total of the 9 ears is only 47.7 ± .6. The deviation from the expected 50 per cent. is nearly four times the probable error, indicating a poor fit. The percentage of colorless grains is 48.4 and the deviation is two and two thirds times the probable error. Here the separation is accomplished with a somewhat greater degree of accuracy. On the whole, the data seem to show conclusively that we are dealing with a linkage between waxy endosperm and one of the aleurone factors.

Ear No. 10, which is derived from a non-linkage family and included in the table for comparison with the first nine ears, is also the result of a back cross. The per cent. of crossing over is 49.3, which is practically equivalent to independent inheritance. The deviation from 26.7 per cent. of crossing over is 16.74 times the probable error and the odds against this being due to random sampling are enormous.

EVIDENCE THAT THE *C* FACTOR FOR ALEURONE COLOR IS CONCERNED

Although the linkage data are interesting and valuable, it is perhaps of greater interest and value in the study of maize in-

heritance to know which of the aleurone factors is concerned in this linkage. This may be determined, where the inhibitory factor *I* is not concerned, by crossing plants grown from either colorless waxy or colorless corneous grains taken from families showing linkage with plants that are homozygous recessive in turn for one of the aleurone factors and homozygous dominant for the remaining factors. Plants of this nature were available in Professor Emerson's aleurone testers.

At least five factors are now known to be concerned with development of aleurone color. They are known as the *A*, *C*, *R*, *Pr* and *I* factors. *A*, *C* and *R* are necessary for the development of red. The dominant *Pr* factor changes red to purple. That the *Pr* factor is not concerned in this linkage is evident from the fact that the linkage relation is observed in segregations of colored and non-colored aleurone and waxy and corneous endosperm regardless of whether they are purple or red, and from the fact that only red aleurone seeds were used in obtaining the back cross data which show the linkage. That the inhibitor is not involved is inferred from the fact that the segregation on the original parent ear was 195 corneous colored, 95 corneous colorless, 95 waxy colored and 15 waxy colorless which is approximately a 3 : 1 segregation of colored to colorless aleurone. The relation of the *A*, *C* and *R* factors to waxy endosperm remains to be accounted for. This may be determined as stated above by the use of aleurone testers, which are named for the pair of factors which is homozygous recessive. The following diagram explains the method of testing for these factors.

Constitution of Aleurone Testers	The Constitution of Colorless Grains from the 3 : 1 Ear may be		
	aaCCRR	*AAccRR*	*AACCrr*
A tester, *aaCCRR*	No color	Color	Color
C tester, *AAccRR*	Color	No color	Color
R tester, *AACCrr*	Color	Color	No color

If the *C* factor were linked with the factor for waxy endosperm no color should appear in the F_1 from a cross between the *C* *R* and *A* testers colored ears should be obtained. Crosses of this nature were made in 1916 and 1917 with the following results:

Colorless Aleurone with *C* Tester

Year	Parentage	Approximate Number of Seeds	Color of Aleurone
1916.....	1 (2) × 6857 (9)	360	No color
1916.....	2 (14) × 6857 (12)	240	" "
1916.....	2 (9) × 6857 (4)	500	" "
1917.....	101 (1) × 7506 (2)	250	" "

Colorless Aleurone with *R* Tester

Year	Parentage	Approximate Number of Seeds	Color of Aleurone
1916.....	1 (5) × 6867 (19)	480	Colored
1916.....	2 (1) × 6868 (6)	200	"

Colorless Aleurone with *A* Tester

Year	Parentage	Approximate Number of Seeds	Color of Aleurone
1917.....	101 (7) × 7505 (2)	150	Colored

The above data are believed to show conclusively that the *C* factor for aleurone is linked with the factor for waxy endosperm, because the *R* and *A* testers caused the development of aleurone color when crossed with colorless individuals from the same family while the *C* tester did not.

Non-Linkage of Aleurone Color and Waxy Endosperm

It is interesting to know that in ear 10, which shows no linkage, the *C* factor for aleurone was not heterozygous. A colorless waxy individual from this family crossed with the *C* tester produced an ear consisting of approximately 300 seeds, all of which showed colored aleurone.

Another waxy colorless individual of the same family crossed with the *R* tester produced an ear with 25 seeds, all of which were colored. Thus the *C* and *R* factors are eliminated with some degree of assurance. The *A* factor apparently is heterozygous in this family, but unfortunately the writer has obtained no crosses with the *A* tester to verify the conclusion reached by the process of elimination. This may be considered as indirect proof of the *C* factor as the aleurone factor which is linked with the waxy endosperm factor.

Summary

(*a*) Collins has presented conclusive evidence of the linkage between waxy endosperm and aleurone color. The writer has presented additional evidence from back crosses, which shows the

intensity of the linkage in the material at his disposal to be equivalent to 26.7 per cent. of crossing over.

(*b*) It has been shown directly, by means of crosses between colorless individuals in a linkage family and aleurone testers and indirectly by means of aleurone tests with a non-linkage family where the *A* factor and not the *C* factor is heterozygous, that the *C* factor for aleurone is linked with the factor for waxy endosperm.

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INHERITANCE IN ORTHOPTERA

IN a recent paper (Nabours, '17) Nabours has continued his admirable studies of inheritance in *Paratettix*. The paper is backed up with an abundance of data, from which a number of facts are deduced. In his discussion, he attacks certain modern hypotheses, and since it appears to me that his strictures are not entirely justified, I venture here to review the evidence, and make certain comments on it.

The following facts, several of which were well brought out in a previous paper (Nabours, '14), are presented:

1. A large number of distinct, true-breeding forms of *Paratettix* occur "in nature." Of these he has collected at least fourteen or fifteen. He no longer looks upon each as a distinct species, and he has dropped the "specific names" he suggested for them in the previous paper.

2. The distinguishing characteristics of these forms fall into two groups in their mode of inheritance: (*a*) Fourteen color patterns act as allelomorphs to each other. (*b*) A fifteenth pattern is "allelomorphic only to its absence."

3. One of the characters of the "multiple allelomorph" group does not always act as an allelomorph to the other members of the group. This is the character I of his first paper, which was noted then for the same behavior. Rather, it behaves (to put it briefly, but in words very different from Nabours's) as if it were closely but not completely linked to the others.

Because I wrote a review of Nabours's first paper on this subject (Dexter, '14), I feel a certain responsibility for what I think are mistaken viewpoints concerning the multiple-allelomorph-nature of this group.

Bellamy, working in the same laboratory, contributes also an excellent study on the same subject, but based on a different genus of *Tetrigince* (Bellamy, '17). Both he and Nabours have apparently accepted as proven that there is here a large group of determiners allelomorphic to each other, and I am quoted in support of this idea. Inasmuch, however, as I made certain reservations which are important in the light of the new data presented, I beg to quote a portion of my former paper.

> As Sturtevant has pointed out, for any case to which the idea of multiple allelomorphism is applicable, an equally valid explanation may be found in "complete linkage" of the factors concerned. To decide in any case between the two explanations would be impossible. If however linkage were not complete, a "cross-over" class . . . might occur, and this would suffice to rule out the explanation based on multiple allelomorphs. Such a cross-over class perhaps is furnished by the BEI individual.

I then suggested that since the BEI individual had been lost before it could be tested, the cross be repeated, and said:

> If then BEI forms should occur again, and in these, when mated to other forms, the factors B and I should be found to stay together to the same extent as before they separated, it would show that close linkage rather than multiple allelomorphism explains this particular instance.

Nabours has repeated this experiment, using the character S instead of E, and has again obtained such a cross-over, BIS. With this individual, he has carried out breeding tests.

Apparently forgetting what had been pointed out in my paper, he says:

> The significant feature is the complete combination or linkage, apparently permanent, of the factor for S, and the factor for the modified I. . . . This combination, IS, becomes a new form, *a new multiple allelomorph* (italics not original), pairing with and allelomorphic to any other multiple allelomorph with which it has been tried. . . . It is not possible for me to suggest the means by which the combination or linkage was effected.

(One must protest against the use of words which permits a single determiner to be called a "multiple allelomorph.")

The answer that he was unable to give is obvious. Perhaps there are thirteen characters here whose determiners are allelomorphic to each other. That is possible, perhaps probable,

though unproved. But I is not a member of that group, but is only linked to it, being, as we may say, in the same chromosome. The work that Nabours has done makes that certain, and disposes also, by the way, of the likelihood that non-disjunction explains the similar case in the first paper (Bridges, '16).

Nabours has made a sort of mystery of the character called G in his first paper, but now called θ, which, he says, is "only allelomorphic to its absence." Ignoring the philosophy of this statement, he has shown that θ mendelizes independently of the other characters. He suggests that such determiners may be of frequent occurrence. He has shown that by substituting Greek letters for English letters the formulæ will work out as well as they did before, and has naïvely applied the method to the case of comb inheritance in poultry. His difficulty is simply caused, and Bellamy has pointed out its solution:

> It need only be assumed that the determiner is borne by some other chromosome.

In *Drosophila* some four or five years ago, the determiner for bent wings was the only one known for the fourth chromosome group. If at that time we had known only one other set of characters in *Drosophila,* viz., that of the white-eosin group, the situation would have been parallel to the one described by Nabours. We might speak of a half dozen or so of "characters allelomorphic to each other," and of one, bent, "allelomorphic only to its absence." Later on, when we found other characters whose determiners were located in the fourth chromosome, we should modify our theory. Nabours's industry in his research makes me feel safe in prophesying that he will yet discover something linked to θ.

He says parenthetically that two other characters "apparently of the nature of θ" have been discovered. It is important to find out their linkage relations and we shall wait eagerly to hear of them. In the meantime we must conclude that he has discovered the beginning of at least two chromosome groups.

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INTERNAL FACTORS INFLUENCING EGG PRODUCTION IN THE RHODE ISLAND RED BREED OF DOMESTIC FOWL

A SURVEY OF THE PROBLEM OF EGG PRODUCTION AND A PRELIMINARY ANALYSIS OF AN EGG RECORD INTO ITS CONSTITUENT ELEMENTS

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INTRODUCTION

A SURVEY of the problem of egg production, such as is made in the present paper, seems desirable at the present time because of the great interest taken in breeding for increased egg production. While the various factors discussed are familiar, to a degree at least, to most poultry keepers, nevertheless they are ignored in breeding practise and reliance placed upon the numerical record alone as a sufficiently detailed and accurate description of a hen's performance, although, as will be pointed out in a later section, identical numerical records result from quite diverse combinations of factors.

The point of view which we have been led to adopt may be stated in one form as follows: The *egg record* of a hen, expressed as a given number of eggs per unit of time and taken by itself, is not a sufficient measure or description of egg production, even under a favorable environment, for the record is the result of the interaction of a number of innate factors. Some of these factors, such as rate of growth, are quite distinct from egg production, while

others, such as rhythm, are almost inseparable from egg production itself. The numerical record of a hen shows only the number of eggs laid, but does not show the component elements which enter into the making of such a record. All these various elements must be studied individually and the influence exerted by each on egg production worked out. Moreover, the mode of inheritance of the separate factors must also be determined.

Further, it should be noted that the interrelation of the various factors is so complex that it is difficult to describe each by itself. In nearly all cases the bearing of some other factors must be considered to a certain extent, at least, along with that factor which is specifically under discussion.

It is important to observe that while the results obtained for the Rhode Island Reds described in this paper differ in several respects from those obtained by Pearl ('12) for Barred Plymouth Rocks, these differences are inherent in the birds themselves and are on a par with the visible differences, such as color, that exist between the two breeds. Pearl has anticipated that differences in fecundity in various strains and breeds are likely to be found. He states as follows:

> The writer has no desire to generalize more widely from the facts set forth in this paper than the actual material experimentally studied warrants. It must be recognized as possible, if not indeed probable, that other races or breeds of poultry than those used in the present experiments may show a somewhat different scheme of inheritance of fecundity. . . . I wish only to emphasize that nothing is further from my desire or intention than to assert before such investigations have been made that the results of the present study apply unmodified to all races of domestic poultry.

It is clear, then, that a complete knowledge of fecundity and its inheritance in domestic birds can only be obtained by a careful study of egg production in all breeds and perhaps even in several strains of the same breed. As shown later on, one of the several factors that determine winter egg production is characteristic of Pearl's

Barred Plymouth Rocks, while another is characteristic of my Rhode Island Reds.

The data in this paper are obtained from a flock of 220 March and April hatched pullets placed in the laying houses in the fall of 1913, together with the data on winter egg production from the flock (numbering 482 pullets) placed in the laying houses in the fall of 1915, although the composition of this flock was not the same as that of 1913–14, because it had been altered by the addition of several other strains in order to overcome the unsatisfactory vitality of the original flock. The addition of new blood apparently increased the variability in some respects as shown by the statistical constants (*cf.* Figs. 1 and 2, also 10 and 10*a*). The winter production of the flock of 1914–15 was decidedly poor and apparently not normal, probably due largely to environmental conditions, and hence data from this flock have not been used.

It is impossible within the limits of this paper to present detailed data on all points discussed. To the reader who is unfamiliar with egg records, it may be said that an inspection of the records reveals the essential nature of the problems.

The original flock came mainly from one of the leading showroom strains of the country, to which were added a few individuals from another showroom strain. Neither strain, so far as known, had been especially bred for egg production, nor had any of the strains added in 1915.

Ways of Measuring Egg Production

It has been customary in times past to determine a hen's egg production by her record expressed in the number of eggs per year, the year usually running from November 1 through the succeeding October 31. At other times the first-year record of the hen has been taken as the time unit, beginning with her first egg and running 365 days therefrom. More recently, the Maine Experiment Station has used the period beginning with the first egg of a pullet and extending to March 1 as the unit of

measurement, since March 1 serves as a convenient calendar date, near the end of the winter cycle. Still more recently the same workers have suggested that even a shorter period would be desirable, because it is held that a hen only reaches her highest possibilities under favorable conditions. Recently the Utah Station (Ball, Turpin and Alder, '14) has suggested that for Leghorns the records be kept for three years, since hens that lay poorly the first year often lay much better during the second or third. Rice, however, ('13) has published data on this point, which show that such birds are the exception rather than the rule.

A year, however, may be considered to be a natural unit. During this period the whole cycle of seasonal changes is gone through with. Moreover, this period bears a definite relation to the bird's life cycle, for its beginning may be taken to correspond to the beginning of egg production in the fall, while its close roughly corresponds to the cessation of egg production the next fall, usually coinciding with the onset of the fall moult, though, of course, in some individuals, the biological year exceeds 365 days. Thus, the year would seem to mark a pretty definite period in the life of the bird as to her innate capacity for egg production. In this paper we have used both winter and annual periods as measures of production, as the necessities of the moment required.

There are some objections to each of the two common methods of determining the point at which the year begins. If the year begins with the first egg of each individual, the differences in age at which the first egg is produced are neglected. If a given point in the year is chosen and the production of all individuals within a year from this date recorded, differences in time of hatching are neglected. Possibly a more satisfactory method would be to take 365 days from the beginning of egg production in each flock of equal age, or else from the average date at which production begins.

The terms "high producer" and "low producer" are

frequently encountered, but each is used very loosely. The use, either of the term "higher producer" or "low producer" without qualifications of any sort can scarcely be considered sufficiently precise. Unless qualified by the word annual, the term "high producer" in this paper will be understood to refer to the winter record only. Pearl ('12) has defined a high producer as a bird that lays over 30 eggs during the winter, a mediocre producer as one that lays during the winter but that lays fewer than thirty eggs, while a zero producer does not lay at all during the winter. As will appear later, the use of the numerical value of the record as its sole characteristic is insufficiently precise. The term "true mediocre producer" will be used to denote a mediocre producer in the sense (Pearl's) explained below, while the term "mediocre (under 30 eggs) producer" will be used elsewhere.

The Influence of External Factors.—A brief consideration of the relation of external factors to egg production is necessary before considering internal factors.

External factors may be divided into two classes: first those that operate rather directly upon egg production, and secondly those that operate indirectly, through their influence on the organism as a whole.

Under the head of direct factors should be mentioned housing, climate, food, general care, etc. It should go without saying that the birds must be properly fed and kept under conditions generally recognized as suitable for maximum egg production. It is not yet clear, however, that the optimum conditions are fully known, or that they can be obtained at will, for with the present appliances for keeping poultry, only the crudest sort of approximation can be made toward securing a uniform environment. For example, one is never certain with open-front houses that a draft may not strike one portion of the flock, while on the roosts, but not another. There are many little things of this sort which can not at present be controlled, nor is it definitely known in what way these "little things" influence egg production. Some

appear to be without any influence whatsoever; others appear to be of varying degrees of importance.

Thus, it is not easily possible to overemphasize the importance of the environment in relation to egg production. At best, certain elements of the environment are partially controlled and *similar* conditions supplied to the members of the flock under experimentation, but it is impossible with the best practical facilities at present available to furnish *identical* conditions to all individuals of the same flock. At the very best one can only go through the motions of providing such conditions. Moreover, one may be forced to modify the procedure selected in order to keep the birds in good condition. Furthermore, *individuals* or *strains* may not react in the *same fashion* to *identical conditions.*

The difference in the reaction of individuals of the same strain to similar conditions, particularly when these conditions fall near the critical point for the strain (or species), is a matter of considerable importance, especially when a character such as egg production is under study, and more especially when it is impossible to control certain important elements of the environment. As long as the environment is not too far from the optimum, birds of low vitality, for example, may do quite as well as birds of much higher vitality, but when the environment approaches either end of its range, then its effects begin to manifest themselves.

A full discussion of the possible influence of the environment, either directly or indirectly, upon egg production as a whole or upon any of the several factors influencing production is outside the scope of this paper. While the reader should bear in mind the possibility that the environment has introduced disturbing factors, every effort has been made to keep all controlable elements, such as feeding and housing uniform.

Turning now to internal factors, we find that these also may be considered under two heads. We have little to do with the factors falling under one of these heads, for

their effect is exerted only indirectly. They undoubtedly play an important part in egg production, but like many external factors they are without influence unless they fail in some way. Such factors are the capacity to digest and assimilate food, to excrete waste matters properly, etc. It is not my purpose at this time to discuss such factors. Those internal factors with which we are mostly concerned are those whose relations to egg production are much more obvious. They are rate of growth of the chick, cessation of growth, the attainment of both bodily and sexual maturity, moults, the size of the bird, the stamina of the bird, the presence or absence of cycles, litters or clutches of production, the rhythm of production, the rate of production for definite time intervals, age at first egg, and broodiness. Some of them are clearly separable from egg production. Others are so closely interwoven that it is impossible to say that they are not phases of egg production. Whether or not this is so, is of no immediate importance from the standpoint of inheritance, since the result will probably be the same whether they are treated as genetic factors that are separable from egg production or treated as groups into which egg production itself may be divided. These factors may be regarded as phases of egg production if one desires, but on the whole it has seemed profitable to regard them as factors influencing egg production.

Rate of Growth, Bodily Maturity, Cessation of Growth, Sexual Maturity[1]

These interrelated factors are closely interwoven in their effect on egg production. Under normal conditions it is clear that sexual maturity is indicated by the beginning of egg laying, and may be measured by a bird's age at her first egg, *i. e.*, the length of time elapsing between the date hatched and date of first egg. Sexual maturity, however, demands certain antecedent conditions before it can become manifest. Among other conditions is a cer-

[1] Unless otherwise stated, reference here is to the female only.

tain body size, which depends upon the rate at which the individual grows, as well as the limiting size for that individual. That is, size at a given age is the result of rate multiplied by time, up to certain limiting values determined by the genetic composition. Cessation of growth, however, does not necessarily coincide with the onset of sexual maturity nor even with general bodily maturity. Although it is certain that the hen is heavier in her second autumn than at the beginning of egg production, our data show that there is little or no growth during the first winter. We must, then, distinguish between sexual maturity, which is capable of manifesting itself as soon as the body reaches a certain size, from that maturity which is not attained until long after the adult size is reached. At present the relation between sexual maturity and bodily maturity has not been worked out. Some extreme phases, however, of the interrelation appear a priori probable. Chicks that grow very rapidly naturally tend to reach sexual maturity at a very early period in their life. They may or may not start in laying immediately after reaching full size. Other birds grow very slowly and can not lay before a certain size is reached. Therefore, they must of necessity reach sexual maturity relatively late in life. It may be impossible for birds of this sort to reach sexual maturity before spring if hatched during the usual breeding season (April, May). The general effect of slow growth, then, will be to lower the record made by such individuals, although they may be otherwise identical with those that grow more rapidly.

Combined with the factors mentioned are the factors that limit the size finally reached. As pointed out above, size results from rate of growth times length of period through which growth continues. Each factor is determined in part by the environment and in part by the genetic constitution of the bird.

The following combinations of factors (Table I) and their effect on egg production may be *assumed*. Each factor is treated as though it were wholly independent

of the others. Early sexual maturity is assumed to be a constitutional tendency to begin laying as soon as a sufficient body size or body maturity is reached, while late sexual maturity is assumed to be a tendency to delay production until after body maturity is attained. This heading, however, does not refer to the objective attainment of sexual maturity which is shown by the column on "time of first egg." The length of the growth period also is assumed to be determined by the attainment of bodily maturity.

TABLE I

VARIOUS COMBINATIONS OF HYPOTHETICAL GROWTH FACTORS WITH THEIR EFFECT ON WINTER EGG PRODUCTION

Rate of Growth	Sexual Maturity	Growth Period	Probable Time of First Egg	Probable Winter Egg Production
Rapid	Early	Short	Early	High
"	Late	Short	Late	Low
"	Early	Long	Relatively late	Medium
"	Late	Long	Late	Low
Slow	Early	Short	Relatively late	Medium
"	Late	Short	Relatively late	Low
"	Early	Long	Late	Low
"	Late	Long	Very late	Zero

It appears from this table that early sexual maturity can become fully effective only when combined with rapid growth during a short growth period.

The effect of the activities of some of these factors as bearing on winter egg production may be given more specifically as follows: If we measure egg production by the number of eggs laid before the 1st of March, assuming for the moment that this point represents, approximately at least, a definite point in the history of the egg production of each individual, it follows that the birds hatched during April and May, or to take a definite point for the purposes of illustration—April 15—which mature at five months, as is sometimes the case, will begin to lay September 15 and will lay a large number of eggs before March 1, provided, of course, that they do not moult. On the other hand, true mediocre productivity (slow rate) associated with early maturity will tend to force a bird

out of the class of mediocre producers, when measured by a specific number of eggs, into that of the high class. If, then, one is dealing with a flock in which these degrees of maturity exist, it is evident that extreme care must be taken to avoid confusion due to differences in maturity or rate of growth.

Differences in maturity may be observed among the males as well as the females, although there is no precise objective point at which a male may be said to have become mature, which is comparable to the first egg of a pullet. On the whole, the larger birds tend to mature later than the smaller, though the rule is by no means rigid, since some small birds grow slowly while some large birds grow quickly. Since age at first egg is so large a factor in determining the kind of record a bird makes, one has a physiological character in the male of considerable value as an index of his capacity for producing females that will mature at a given age.

The age of a bird when she produces her first egg does not coincide necessarily with bodily maturity, theoretically at least, although it seems that a certain size must be reached before the bird can begin to lay. On the other hand, the relation between body size and age at first egg as frequently encountered is of a sort such that the larger birds tend to lay at a later absolute age than the smaller ones hatched the same day. There are many exceptions, however, to this rule. It would, perhaps, be better expressed to say that more heavy birds lay late in life than early, while more of the lighter birds lay early than late. For one of the flocks, the coefficient of correlation between age at first egg and weight has been calculated and found to have a value of $+.5473 \pm .0216$.

The influence of the date at which the first egg is produced as well as the relation of age at first egg to the number of eggs laid during the winter months is shown in the series of records shown in Figs. 3 and 4 (Page 78). These records have been selected in such a way that the rate of production is nearly constant, although the date of hatch-

ing of the individual birds covers a period of five weeks. The records are to be read as follows: The number in the upper left-hand corner is the hen's number. The *vertical* mark in *each* square indicates that an egg was produced on that day. The totals are given for each month while the figure at the extreme right of the row headed

FIG. 1.[8] Graph showing the percentage of the flock beginning to lay at the age (in days) indicated by the class limits. Flock hatched in March, April and May, 1915. M = 263.19, S. D. = 37.71; $C. V._2 = 43.00$, $C. V._1 = 14.33$.

"February" is the total number of eggs for the winter period. The records for March and April have also been included in order to show the type of record made by birds that begin to lay very late in the season. These records show clearly that no sharp dividing line exists in the number of eggs laid. On the contrary, it is clear that birds hatched at the same time begin to lay at widely different dates and that in consequence differences in egg yield for the winter period result. That this result is of general applicability to our flocks is shown by the fair

[8] In calculating the $C. V._{(2)}$ for the data given in Figs 1 and 2, the mean was taken as the difference between the mean age and the lower end of the range of Fig. 1.

amount of homogeneity in the flocks in respect to rate of production as described below.

Graphs showing the age at first egg for the flocks of 1913–14 and 1915–16 are shown in Figs. 1 and 2. The former (Fig. 2) is unimodal and has a narrow base, the shape of the curve indicating a high degree of homo-

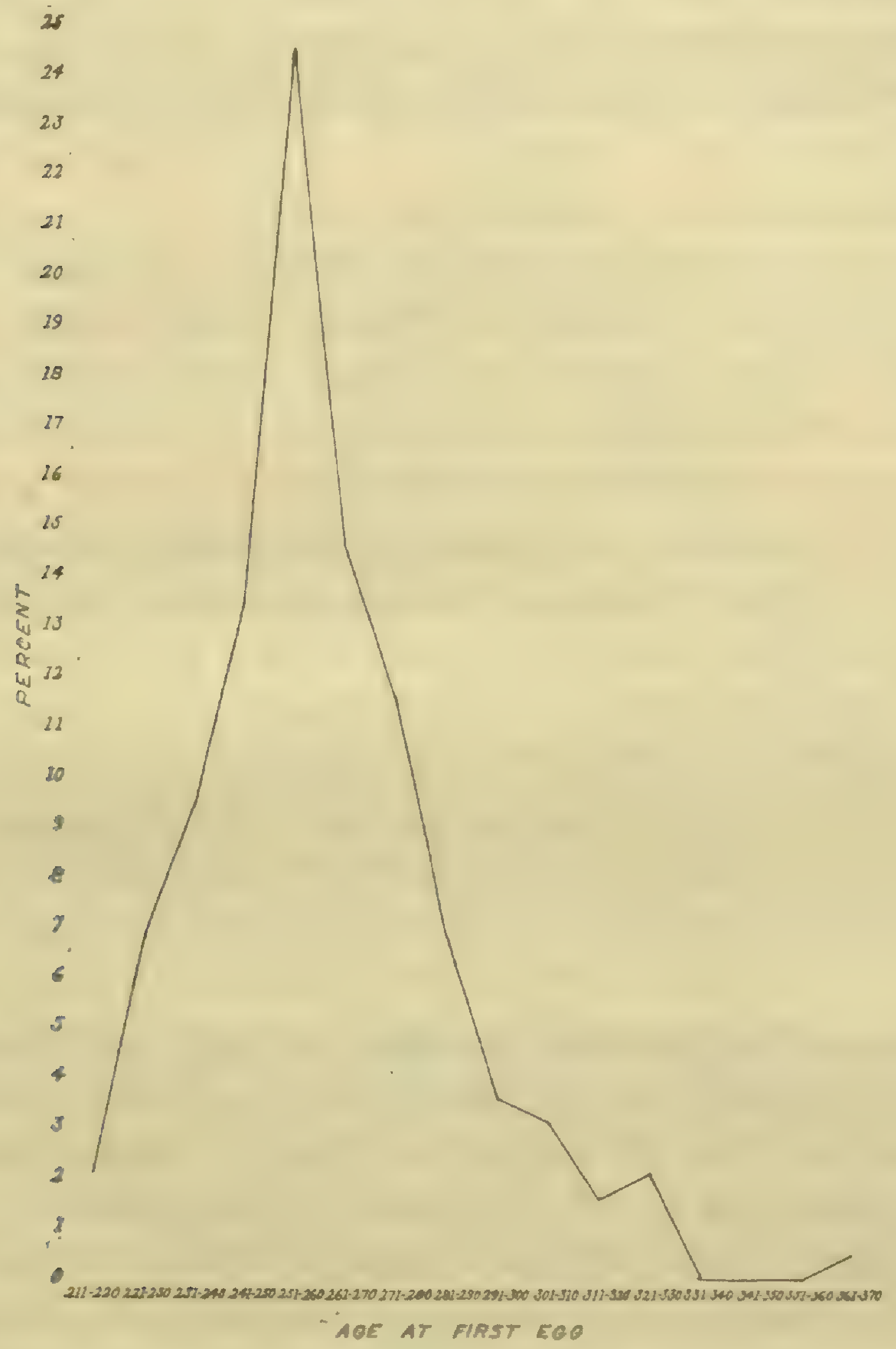

FIG. 2.[8] Graph showing the percentage of the flock beginning to lay at the age (in days) indicated by the class limits. Flock hatched in March and April, 1913. M = 261.18, S. D. = 24.34, C. $V._2$ = 28.41, C. $V._1$ = 9.32.

geneity in the flock. As might be expected from the nature of the data (which is affected by the environment in only one direction, *i. e.*, toward a retardation of the age at first egg) the lower part of the right-hand side slopes

off more gradually than the left. The mean has a value of 261.18 days.[2]

The curve for the flock of 1915–16 (Fig. 1) is somewhat unlike the preceding. It is distinctly bimodal, but it is not altogether clear that this bimodality indicates two genotypes, for it may be due to chance alone. The base is broader than for the 1913–14 curve, indicating less homogeneity of the flock in this respect, although the same gradual slope on the right-hand side is apparent. There are reasons, however, for believing that the left-hand side of the graph for the flock of 1913–14 was shortened by the methods of handling the pullets that fall. The mean has a value of 263.18 days. The difference between this graph and the first is undoubtedly due to the changes in the composition of the flock as described in an earlier paragraph.

Graphic representations of the day on which the various members of the flock produced their first egg are shown in Figs. 5 and 6. The data for the two flocks, *i. e.*, 1913-14 and 1915–16, are divided into groups according to the month in which the pullets were hatched. Each dot in the figure represents the first egg of a pullet and is placed in a square corresponding to the date on which the egg was laid. If more than one pullet began to lay on a given date, there is a dot for each pullet.

There are some interesting differences and resemblances between the groups mentioned in the distribution of the first egg through the various months. In all instances the pullets laying for the first time come in slowly during the first few weeks. Then follows a period of six to eight weeks during which the new pullets come in at a faster and fairly uniform rate. This period is followed by a third period when new pullets come in slowly, the last of the period representing the stragglers. The fairly uniform scatter is due in part to the inclusion of several

[2] In this paper we have given only those statistical constants that appear to be particularly pertinent and as a rule have omitted the probable error, especially where "*n*" is large, unless there has been special reason for inserting it.

No. 4846 HATCHED MARCH 21, 1915. AGE AT FIRST EGG, 191 DAYS

Date 1915–16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Sept.																												/	/		■	2	
Oct.	/	/		/		/		/	/	/		/	/	/	/		/	/	/	/		/	/		/	/		/	/	/		22	
Nov.	/		N	/		/	/	/		/	/		/	/		/	/		/	/		/	/	/	/		N	/	/	/	■	20	
Dec.		N	/		/		/	/		/	/	/	/		/	/	/		/	/		/	/	/		/	/	/		/	/	21	
Jan.	/	/		/	/	/	/		/	/	/		/	/	/		/	/	/		/	/		/		/	/		/	/		22	
Feb.	/	/		/	/		/	/		/	/		/	/		/	/	/		/	/	/		/	/		/	/		■	■	20	107
Mar.	/		/		/		/	/		/	/		/	/		/		/		/	/		/	/		/		/		/		18	
Apr.	/	/		/	/	/	/		/	/	/	/		/	/	/	/		N						N			N N	N	N	■	14	

No. 4921 HATCHED MARCH 21, 1915. AGE AT FIRST EGG, 219 DAYS

Date 1915–16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Sept.																															■	0	
Oct.																										/		/		/		3	
Nov.	/		/		/		/	/		/		/		/		/		/	/		/		/	/		/	/			/	■	17	
Dec.	/	/		/	/		/	/	/	/			/	/	/	/	/		/		/	/	/	/		/	/	/	/	/	/	24	
Jan.		/	/	/	/		/	/	/		/	/		/	/		/	/		/	/		/	/	/		/	/	/		/	22	
Feb.		/	/		/		/		/		/	/		/		/	/		/	/	/		/	/		/	/		/	■	■	18	84
Mar.	/	/		/	/	/	/	/	/		/	/	/	/		/	/	/	/	/	/		/	/	/	/	/	/	/	/	/	27	
Apr.	/		/	/	/	/	/	/	/	/	/		/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	■	28	

FIGS. 3 AND 4. Daily records of Rhode Island Red pullets hatched in 1915, arranged in order of decreasing total winter eggs to show the effect of approximately equal rates of production, but of different dates of first egg on the total winter production, as shown by the numeral at the right of the February record. March and April records are included to show that no fixed date can be selected as a dividing line. l = an egg; N = on nest but did not lay; B. L. = removed to broody coop; A = returned to pen.

No. 4514 HATCHED MARCH 7, 1915. AGE AT FIRST EGG, 266 DAYS

Date 1915–16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Nov.																								N			N	/		/	■	2	
Dec.	/		/	/	/		/		/	/		/	/		/		/	/		/	/		/	/		/	/		/	/		20	
Jan.	/	/		/	/		/	/		/	/		/	/		/	/		/	/		/	/		/	/		/	/		/	21	
Feb.	/		/	/		/	/		/	/		/	/		/	/		/	/	/		/	/	/		/	/	/		■	■	20	63
Mar.	/	/		/	/	/		/	/	/	N.	/	/	/	/		/	/	/		/	/	/		/	/		/	/	/		23	
Apr.	/	/	/		/	/	/	B L					A N				/		/	/	/		/	/	/		/	/	/	/	■	17	

No. 5297 HATCHED APRIL 11, 1915. AGE AT FIRST EGG, 268 DAYS

Date 1915–16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Nov.																															■	0	
Dec.																																0	
Jan.				/	/	/		/	/	/	/		/	/	/		/	/	/		/	/		/	/		/	/	/		/	21	
Feb.	/		/	/			/	/		/	/		/	/		/	/	/		/	/		/	/	/		/	/	/	■	■	20	41
Mar.		/	/		/	/	/		/	/	/		/	N	/	/		/	/	/		/	/		/	/	/	BL /				20	
Apr.	A		N	/		/	/		/	/	/	/	/	/		/	/	/	/	BL /			A BL				A				■	14	

FIGS. 3 AND 4.—*Continued.*

No. 4620 HATCHED MARCH 14, 1915. AGE AT FIRST EGG, 312 DAYS

Date 1915–16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Nov.																															■	0	
Dec.																																0	
Jan.										/						/	/	/		/	/	N		/	/	/		/	/	/		12	
Feb.	/	/	/		/	/	/		/	/		/	/	/		/	/	/	/		/	/	/	/		/	/	/	/	■	■	23	35
Mar.		/	/	/	/	/		/	/	/	/	/	/		/	/	/	/	/		/	/	/	/	/		/	/	/	/	/	26	
Apr.	/		/	/	/	/	/	/	/	/		/	/	/		/	/	/		/	/	/	/		/	/	/	/	/		■	24	

No. 5180 HATCHED APRIL 4, 1915. AGE AT FIRST EGG, 294 DAYS

Date 1915–16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Nov.																															■	0	
Dec.																																0	
Jan.																							/		/	/	/	/		/	/	7	
Feb.	/		/	/		/	/		/	/		/	/	/	/	/		/	/	/		/	/	/	/		/	/	/	■	■	22	29
Mar.	/	/		/	/	/	N	/		/	/	/	/	/	/	/		/	/		/	/		/	/		/	BL				21	
Apr.	A	N	N				/	/		/	/	/	/	/	/	/	/	/		/	/	/	/	/	/	/	/		/	N	■	20	

FIGS. 3 AND 4.—*Continued.*

No. 5149 HATCHED APRIL 4, 1915. AGE AT FIRST EGG, 304 DAYS

Date 1915–16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Nov......																															■	0	
Dec......																																0	
Jan.......																																0	
Feb......		/		/		/	/		/	/		/	/	/		/	/	/		/	/	/	/	/		/	/	/	/	■	■	21	21
Mar......	/		/	/	/	/	/	/		/	/	/	/	/	/	/	/	/	/	/		/	/	/	/	/	/	/	/	/	/	28	
Apr......	/	/		/	/	/	N		/	/		/	/	/	/	/	/	/		/	/	/	/	/		/	/	/	/	/	■	24	

No. 4568 HATCHED MARCH 14, 1915. AGE AT FIRST EGG, 336 DAYS

Date 1915–16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Nov......																															■	0	
Dec......																																0	
Jan.......																																0	
Feb......													/		/	/		/	/		/	/	/		/	/	/		/	■	■	12	12
Mar......	/	/	/	/		/	/	/	/	/	N	/	/	/	/	/	/		/	/	/	/		/	/	/	/		/	/	/	26	
Apr......	N /		/	/	/	/		/	/	/	/		/	/	/	/		/	/		/	N /		/	/	/		/	/	BL /	■	23	

FIGS. 3 AND 4.—*Continued.*

No. 5192 HATCHED APRIL 4, 1915. AGE AT FIRST EGG, 334 DAYS

Date 1915–16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Nov.																															■	0	
Dec.																																0	
Jan.																																0	
Feb.																														■	■	0	0
Mar.			/		/	/			/		/	/		/	/	/		/	/	/	/		/	/	/	/	/	/	/			20	
Apr.											/	/		/	/	/		/	/	/	/		/	/	/	/		/	/	/	■	16	

No. 5201 HATCHED APRIL 4, 1915. AGE AT FIRST EGG, 352 DAYS

Date 1915–16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Nov.																															■	0	
Dec.																																0	
Jan.																																0	
Feb.																														■	■	0	0
Mar.																					/		/	/	/		/	/	/		/	8	
Apr.	/		/	/	/		/	/	/		/	/	/	/		/	/	/		/	/		/	/		/	/	/	/		■	22	

FIGS. 3 AND 4.—*Concluded.*

HATCHED IN MARCH, 1915

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Per Cent.
Sept.		•			•			•					••			•	•						•	•	•		•	••		••		8.3
Oct.		•	•	•			•	•	••		•		•		•	•		•••			•	•		•	••	•		••	••	•		13.9
Nov.	•	•••	••••	••••		••		•	•••	•	••	••	•	•••	••	•	••••	••	•	••		••		•	•	•	•	•••		•		27.2
Dec.	•••	•	•		•	•••	••••	•	••		•••	•	•	•••	•		•	••	••	•		•	•	••	•	••	•	••		••	•	24.4
Jan.	•		••				••••	•		••	•	•					•		•								•	•	•	•••	••	12.2
Feb.	••		•	••		•				•	•		•	•	•	•				•		•				•			•			8.9
Mar.			•				•		•					•				•	•									•				3.9
Apr.		•																						•								1.1

HATCHED IN APRIL, 1915

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Per Cent.
Sept.																																
Oct.																							•			•						1.1
Nov.					•		•	•		•	•	•		•		••		••		••		••	•	•			••	•••		••••		14.5
Dec.	•	•	•••	•	••	•••	••	••	•		••	••••••	••	•		••••	•••	•	•••		••	•	••	••	•••		•••	••	•••	•••••	•	34.6
Jan.	••		••	•••	•••	•••••			•	•	••	•••	••	•		••••	•			••	••	•	•	••		•	••	•	•	•••		25.7
Feb.	•	•••	•	•				•		•	•	••			•			•	•••		•		•	•	•	•	•		•			12.8
Mar.	•		••••					•	•••	•			•		•	•					•	•					••		•			10.1
Apr.										•																	•					1.1

FIG. 5.

HATCHED IN MAY, 1915

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Per Cent.
Sept.																																
Oct.																																
Nov.																																
Dec.				•			•			•				•				•				•	•	••		••		•		••	•••	12.5
Jan.	•			••••		••		•	•••	•	•		••	••	••	•••		••••	••	••	•••	••	•	•	•••	••	•	•	•••	•	•••	37.5
Feb.	••••	•••••	•••••	••	•••	•		•	•	•	••		•	•••	••	•	••	••			••		•	•••		•		•				32.4
Mar.	•••		•••			••		•••	•				•		•	•		•		•	•	•		•				•				15.4
Apr.	•									•			•																			2.2

FIG. 5.—*Concluded.* Diagram to show the date on which the first egg of each member of the flock was laid. Flock of 1915-16.

hatches on one chart, and also to the ungrouped data, for if the data be grouped in 10-day periods, a curve is ob-

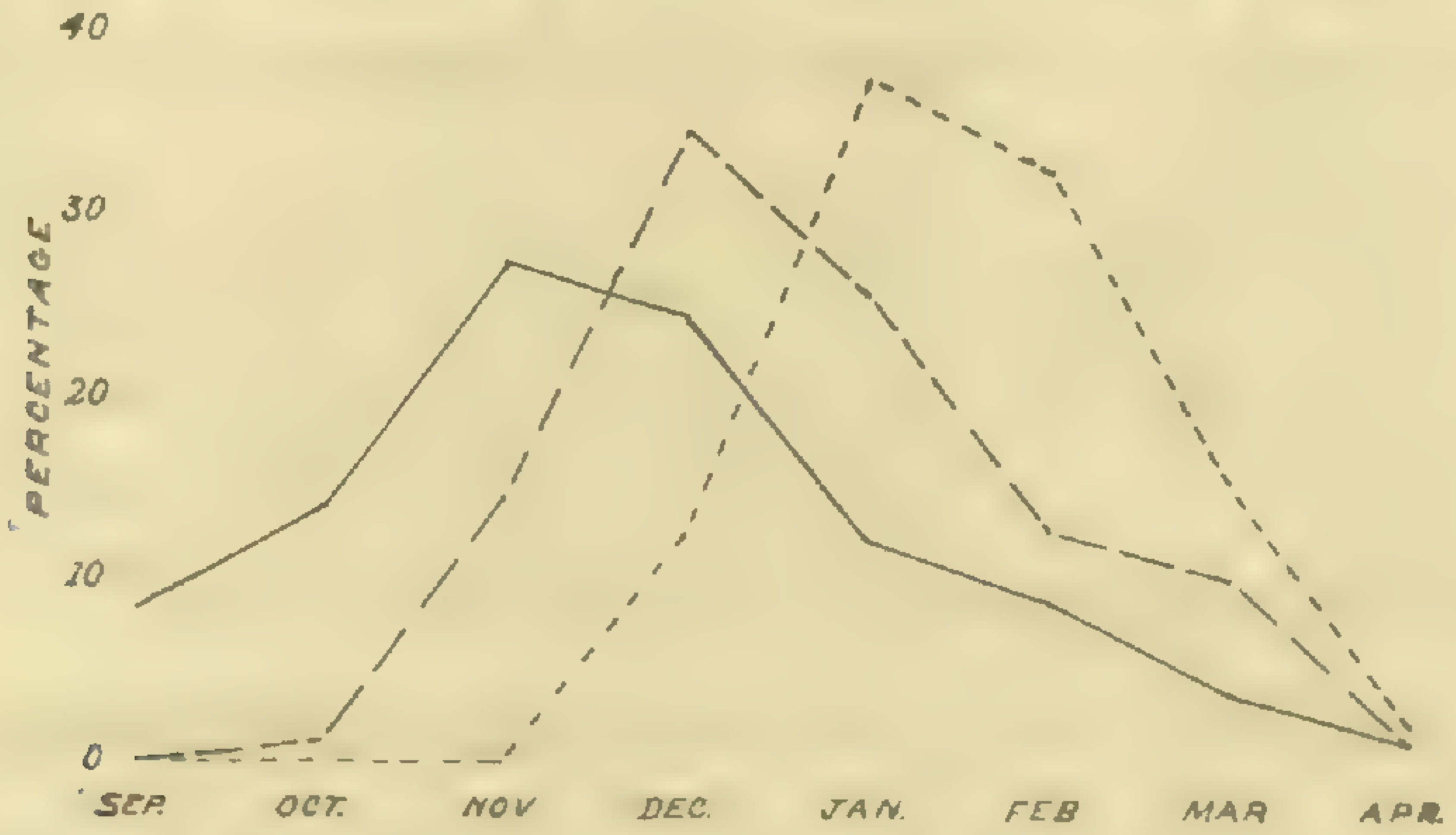

FIG. 5*a*. Graph showing the percentage of the flock of 1915–16 that began to lay in the month indicated. From Fig. 5. ——– March, — — — — April, and - - - - - May hatched pullets, respectively.

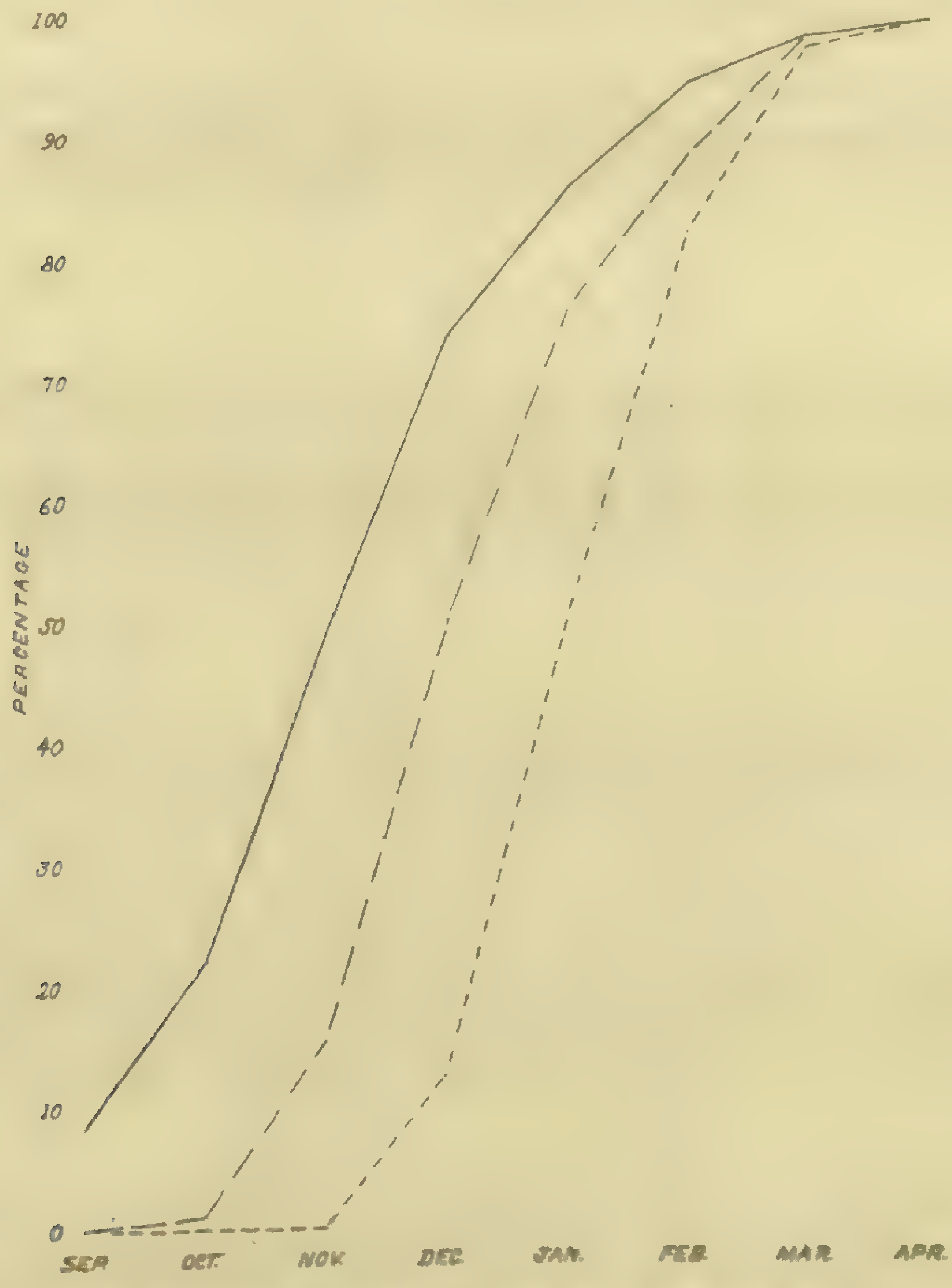

FIG. 5*b*. Graph showing the percentage of the flock of 1915–16 that began to lay during or before the month indicated. From Fig 5. ——— March. — —·— — April, and - - - - May hatched pullets, respectively.

tained similar to the one that results from the combination of the age at first egg curves of several consecutive hatches.

HATCHED IN MARCH, 1913

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Per Cent.
Sept.																																
Oct.																																
Nov.												•		•			••		•					••		•		•	••	•		18.5
Dec.		•	•	•	•••	•	••	•	•	•	•	•••		•••	••		•	•	••••		•	•		•		•		••	••	•	••	58.5
Jan.			•	•		•				•						•	•			•		•				•				•		15.4
Feb.	•								•						•		•															6.2
Mar.																•																1.5
Apr.																																

HATCHED IN APRIL, 1913

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Per Cent.
Sept.																																
Oct.																																
Nov.													•	•	•				••	•		•	•	••	••••	•		••	•••	•		16.5
Dec.					••	•	•	•	••	•	•		•	•	••••	••	••	••	•	••	••	•	•••	•••	•	••	•••	••	•••••	••	•	38.6
Jan.	••••••	•••	•	•••••	••		••	•••	•••	••	•		•	••		••	•	••		•	•	••			•		•	••		•		35.4
Feb.	•	•		•			••	•	•			•								•				•		•						8.7
Mar.	•																															0.8
Apr.																																

FIG. 6.

HATCHED IN MAY, 1913

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Per Cent.
Sept........																																
Oct........																																
Nov........																																
Dec........								•						•				•			•					•		•				25.0
Jan........		•	•	••	•		•			•				•			•				•						•				•	50.0
Feb........				•				•			•			•			••															25.0
Mar........																																
Apr........																																

FIG. 6.—*Concluded.* Diagram to show the date on which the first egg of each member of the flock was laid. Flock of 1913–14.

HATCHED MARCH 22, 1915

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Per Cent.
Sept........																																
Oct........			•					•	••		•					•						•		•					•			25.0
Nov........			•	•											•		•															11.1
Dec........							••		•			•		•								•	•		•	••		•		••		36.1
Jan........	•		•				•••	•				•																				19.4
Feb........	•					•																										5.6
Mar........																																0.0
Apr........									•																							2.8

FIG. 7. Diagram to show the date on which the first egg of each member of the flock was laid. This figure is based on a new sample of the original strain that made their winter record in 1915–16. See text.

In any one hatching group a period of several months elapses between the date the first pullet begins to lay and the date the last member of the flock starts. This period is longest for the March-hatched birds, apparently because the warm spring weather brings all the stragglers to laying and because the March-hatched birds are the first to lay in the fall. For the May-hatched birds the period between first and last pullet is shorter because they begin to lay later in the fall than the March-hatched birds.

For the March-hatched pullets of 1915–16, the initial period is nearly twice as long as for the April or May pullets. The date of the first egg of the first pullet is approximately a month later for the May than for the April pullets. The data, however, for 1913–14 are not quite comparable with those for 1915–16. In the first place it was impossible in 1913, because of lack of room, to begin putting the pullets into the laying quarters until late in October, while some were not finally in place until about the middle of November. The birds therefore did not get settled down at once. The March- and April-hatched pullets both began to lay at approximately the same time and although most (77 per cent.) of the March birds had commenced laying by January, a considerable percentage (viz., 44.9 per cent.) of the April pullets did not begin to lay until after Jaunary 1, which is approximately the same percentage (viz., 49.7 per cent.) obtained for the April pullets of the 1915–16 flock. It should be noted, too, that 73.9 per cent. of the March pullets of this year began to lay before January 1, so that the effect of the delay in housing the 1913–14 flock shows itself principally in a retardation of the first eggs of the March pullets, forcing a larger percentage of first eggs into December than would be normal for that flock. There is a further difference in the two years. The percentage of the April hatched pullets laying after February 1 was about 2½ times as great for the 1915–16 flock as for the 1913–14 flock, the ratio being 24 per cent. for the former to 9.5 per cent. for the latter.

There is another way in which the close relation between age at first egg (also date of first egg) and the winter egg record can be shown, for it follows that the higher the age at first egg the lower the winter record

TABLE II

AVERAGE WINTER EGG PRODUCTION FOR EACH WINTER MONTH OF 1915–16, BY HATCHES

Date Hatched, 1915	Number Pullets in Hatch	Average Winter Production	August	September	October	November	December	January	February
February 7...	12	66.83	5.9	14.3	11.9	5.2	2.6	10.8	16.2
February 14...	8	56.63	5.3	9.9	8.8	6.6	5.5	9.4	11.3
February 21...	13	65.92	1.8	10.5	10.9	10.1	8.8	10.8	13.1
February 28...	18	41.44	0.0	2.0	3.7	6.3	8.8	9.4	11.3
March 7.....	24	44.88	0.0	1.5	5.2	7.2	10.6	10.6	9.9
March 14.....	33	34.15	0.0	0.0	0.8	5.1	7.7	8.3	12.2
March 21.....	48	40.67	0.0	0.3	2.7	7.2	11.6	9.9	8.9
March 28.....	17	40.00	0.0	0.0	0.0	4.4	11.8	12.5	11.3
April 4......	29	29.31	0.0	0.0	0.1	1.0	8.0	9.4	10.7
April 11......	63	31.30	0.0	0.0	0.0	1.9	6.8	10.9	11.8
April 18......	47	29.26	0.0	0.0	0.0	0.6	5.9	10.4	12.4
April 25......	34	27.35	0.0	0.0	0.0	0.4	3.3	10.6	13.1
May 2.......	30	20.27	0.0	0.0	0.0	0.0	1.3	6.9	12.0
May 9.......	30	20.37	0.0	0.0	0.0	0.0	1.8	7.0	11.6
May 16.......	19	18.95	0.0	0.0	0.0	0.0	0.1	4.3	14.6
May 23.......	37	17.78	0.0	0.0	0.0	0.0	0.2	4.6	12.9
May 30.......	20	11.35	0.0	0.0	0.0	0.0	0.3	3.1	8.0

should be. In calculating this coefficient of correlation it is necessary that the birds should all be hatched at the same time, so that for our flocks, which were hatched at intervals of one week, it would be necessary to form as many correlation tables as there were hatches. The probable results did not seem to warrant the labor involved, at

TABLE III

AVERAGE WINTER EGG PRODUCTION FOR EACH MONTH OF 1915–16, GROUPED BY MONTH HATCHED

Month Hatched, 1915	Number Pullets	Average Winter Production	August	September	October	November	December	January	February
February.....	51	56.2	2.7	8.3	8.3	7.1	6.8	10.1	12.9
March........	122	39.8	0.0	0.4	2.3	6.2	10.4	10.0	10.3
April.........	173	29.8	0.0	0.0	0.02	1.1	6.1	10.5	12.0
May.........	136	18.1	0.0	0.0	0.0	0.0	0.8	5.4	11.9

least not at present, so that the coefficient was calculated for one of the largest hatches only. The value found, $r = -.829 \pm .029$, is in full agreement with the hypothesis that the winter egg production of a flock all hatched at the same time, depends largely upon the age at which the first egg is produced.

TABLE IV

AVERAGE WINTER EGG PRODUCTION FOR EACH WINTER MONTH OF 1913–14, BY HATCHES

Date Hatched, 1913	Number Pullets in Hatch	Average Winter Production	August	September	October	November	December	January	February
March 9	10	53.3	......	......	......	3.7	12.7	18.6	18.3
March 16	12	44.8	......	......	......	1.6	11.3	16.8	15.1
March 23	22	47.1	......	......	......	0.3	10.3	19.4	17.1
March 30	17	36.5	......	......	......	0.0	7.7	13.9	14.9
April 6	29	48.6	......	......	......	2.4	11.4	18.0	16.9
April 13	19	41.2	......	......	......	1.2	8.4	16.1	15.6
April 20	37	35.2	......	......	......	0.2	3.3	15.9	15.8
April 27	40	32.5	......	......	......	0.1	4.1	12.5	15.9
May 4	9	42.2	......	......	......	0.0	4.0	19.6	18.7
May 11	13	25.2	......	......	......	0.0	1.3	8.6	15.3

TABLE V

AVERAGE WINTER EGG PRODUCTION FOR EACH MONTH OF 1915–16, OF STOCK FROM ORIGINAL SOURCE

Date Hatched, 1915	Number Pullets in Hatch	Average Winter Production	August	September	October	November	December	January	February
March 22	35	41.11	0.0	0.0	2.3	4.2	7.9	12.8	13.9
April 27	16	23.31	0.0	0.0	0.0	0.0	2.6	8.4	12.3

TABLE VI

A COMPARISON OF THE PROPORTION OF THE FLOCK LAYING EITHER MORE OR LESS THAN 30 EGGS DURING THE WINTER, TOGETHER WITH THE MEANS OF THE RESPECTIVE GROUPS, GROUPED ACCORDING TO THE MONTH HATCHED. THE ZERO PRODUCERS HAVE BEEN OMITTED AND ALSO THE FEW BIRDS THAT LAID EXACTLY 30 EGGS

Month	Over 30			Under 30		
	Av. Winter Production	Number Individuals	Per Cent.	Per Cent.	Av. Winter Production	Number Individuals
February	63.0	43	84.3	15.7	18.8	8
March	54.9	77	68.8	31.3	16.4	35
April	46.3	88	58.7	41.3	16.0	62
May	40.5	29	26.6	73.4	16.1	80

The influence of the time of hatching on winter egg production is shown in Fig. 8 and Table II and III based on the records for 1915–16. The lower graph in Fig. 8 is for birds hatched in March; the middle graph for birds hatched in April; while the upper is for the May-hatched birds. Similar data for 1913–14 are given in Table IV.,

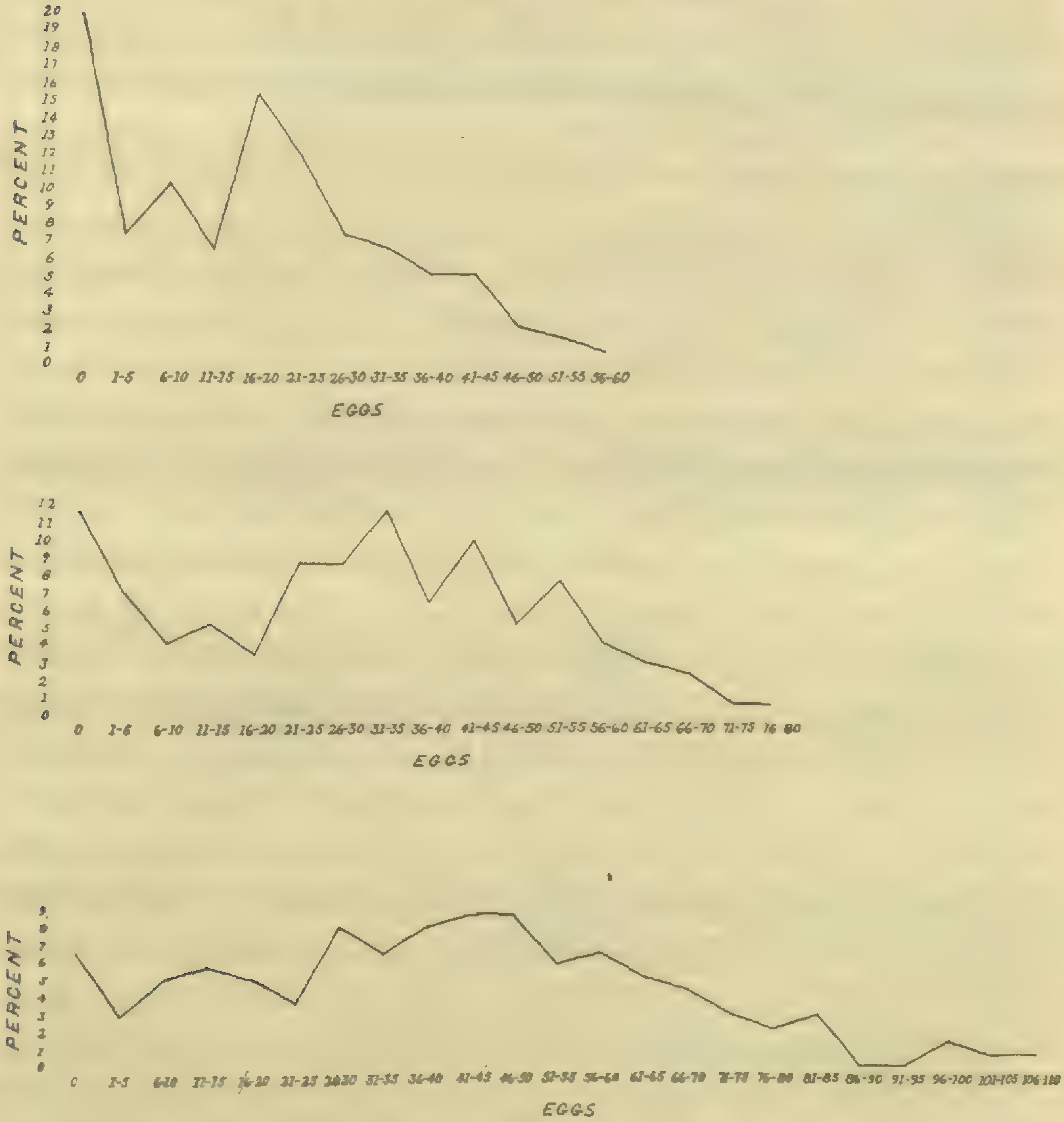

FIG. 8. The effect of time of hatching on winter egg production, the graph showing the per cent. of flock laying the specified number of eggs for the winter period of 1915–16. Lower curve, pullets hatched in March, 1915. Middle curve, pullets hatched in April. Upper curve, pullets hatched in May. M. for March = 42.65, April = 35.4, May = 22.5; S. D. for March = 23.50, April = 17.91, May = 15.58; C. V. for March = 5.5, April = 55, May = 69.2.

It has seemed to the writer that for Rhode Island Reds, the zeros formed a wholly artificial class for reasons given in the text; hence, March 1 marks no natural division point in the time at which the birds begin to lay. Consequently, the zero class has been kept separate and not included in calculating these constants. If M includes the zero class, its value for March is 39.8, for April 29.81 and for May 18.1.

while Table V. should also be examined in this connection. It is clear from these graphs that the earlier hatched birds are superior to the later hatched for winter egg production. In the former group there are fewer zero and more very high producers than in the last. There is also a marked difference in the number of birds in each of the several hatching months that laid over thirty eggs during the winter period. (See Table VI.)

The variability in the age at which the first egg is produced influences the winter record strongly, so much so that we have been led to believe that it is the most important determining factor for egg production during the winter months for our flocks.[3] It leads to the abandonment of the view that those records that fall below 30 eggs are made by true mediocre producers, substituting therefor the view that many, perhaps most, of them are late-maturing high producers. Now, the variability in age at first egg, shown in Figs. 1 and 2, is considerable. If this variability could be eliminated—that is, if it were possible to have each individual of a flock of birds hatched April 1, begin to lay on a definite date, say December 1—the birds would make records which would differ from each other in the proportions given by the graphs of rates of production. The fair degree of homogeneity of the flocks in respect to rate of production is shown in part by the coefficient of correlation between the number of days from the first egg laid up to March 1, and the number of eggs produced during that period. The coefficient was found to have a high value, *i. e.*, for 1913–14, $r = +.8618 \pm .0125$ and for 1915–16, $r = +.7878 \pm .0128$. That is, the number of eggs laid is a fairly definite function of the length of the laying period. These coefficients are a rough index of the amount of homogeneity in the flock respecting the rate of production, since a high coefficient implies a fair amount of homogeneity in the flock (*cf.*, however, the statistical constants for rate) for if an egg a day is taken to represent the maximum production while

[3] The results obtained from our breeding tests substantiate this point.

the minimum is represented by a single egg laid during the winter and that one at the beginning of the winter period, no correlation would exist if the scatter is perfect between these extremes. Experience shows, however, that conditions approached by the maximum rate of production are much more common than those represented by the minimum so that the coefficient, even though it has a high value, shows only that the rate of production is comparatively uniform. It does not prove that the flock is composed exclusively of high producers, for, since it is an average figure, the flock may still contain some true mediocre producers. A certain degree of correlation, however, is to be expected in any flock, so that the mere existence of a small positive correlation is of little value, though a low value for the coefficient would imply that there was considerable variability in rate of production. It is quite clear that if a considerable percentage of the flock made records like those shown in Fig. 12, the variability in rate would be much greater than observed, and the coefficient of correlation between length of laying period and number of eggs would be smaller.

Size.—Size does not of itself seem to have any specific relation to a bird's ability to lay because birds of all sizes may lay equally well once they have started. It is true, of course, that very large birds rarely make high records, but as there are very few large birds, the chance for a combination between very high egg production, itself uncommon, and large size is rather remote. The converse, however, is not apparently true, for small birds frequently make good records. Since, however, birds that are too small are not desired by poultrymen while as a rule large birds are considered desirable, very small birds are not often trap-nested, so that a strict comparison is at present impossible.

In another way size seems to exert some influence on the record a hen makes. On the average, as shown by the coefficient of correlation between age at first egg and weight, birds of large size reach this size later in life

than small birds do. That is, large size usually, but not always, results from long-continued growth rather than from very rapid growth and as long-continued growth naturally tends to postpone the date at which the first egg is laid, the large hen, other things being equal, can not lay as many eggs. It is possible, however, that the case may actually be the converse, viz., the hen may grow large because she does not lay, though there is no definite evidence for this point of view. While it is easy to find many instances of small birds that mature late in life, instances of large birds maturing at the same age as birds of approximately half their body weight have not been observed. The reason for this is probably to be found in the consideration that while some large birds may grow more rapidly than some small birds, it is always possible for some small birds to grow as fast as it is ever possible for a large bird to grow and hence to mature that much earlier.

(*To be continued*)

THE CASE OF THE BLUE ANDALUSIAN[1]

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The blue Andalusian has become the classic in animals as an example of a heterozygote phenotypically intermediate between the parental types. It has also served as an illustration of the failure of dominance for those opponents of Mendelism who consider dominance one of its fundamentals. Furthermore, it has been in constant demand as a classroom example of blended inheritance.

The main facts concerning the breeding behavior of blue Andalusians are, accordingly, more or less familiar. In spite of the long-continued efforts of their breeders they do not come true to color as a breed, but continually throw a certain proportion of off-colored progeny, or "wasters," of two kinds. One is self (entirely) black. The other approaches white, but displays considerable pigment, and is referred to variously as white, splashed, and splashed-white. Since an examination of a large number of birds of this type shows the pigmented feathers to be *blue* in all sections of the female and in those sections of the male which carry blue feathers in the blue Andalusian male, they will be referred to throughout this paper as blue-splashed.

"Splashed" refers to the fact that the pigment does not regularly appear in any particular group of feathers or in any definite region. Feathers located apparently at random on any part of the body may be pigmented over their entire surface or may show only slight traces of pigment. Not infrequently both of these conditions are present in the same individual.

Since the blacks and blue-splashed breed true when

[1] Contribution from the Department of Experimental Breeding, Wisconsin Agricultural Experiment Station, No. 12, and from the Kansas Agricultural Experiment Station.

mated *inter se,* they are considered as being homozygous. If crossed they invariably produce blues.

These facts have led to the current view that the case involves a single allelomorphic pair of characters. The blacks and blue-splashed represent the homozygous conditions, while the self blue is the heterozygote between the two. When blues are interbred, blacks, blues, and blue-splashed are produced in a ratio approximating 1:2:1 for these classes, respectively, which seems to corroborate this view.

Although the blacks and blue-splashed breed true for color, they are not recognized by fanciers as breeds or varieties, and it is doubtful whether they would continue to exist if, much to the disgust of the breeders of blue Andalusians, they did not continue to appear as "wasters" among the progeny of blues. The blues, on the other hand, are quite widely bred. They are officially recognized by the American Poultry Association as a distinct breed and have their place in the American Standard of Perfection. It is interesting in this connection to note that the numbers of blues they throw on the Mendelian expectation barely gets them into the Standard, since the rules of the Association are that no breed can be officially recognized as such unless a minimum of 50 per cent. of the offspring come reasonably true to type (American Poultry Association, 1910, p. 328, Constitution, Article XI).

The blues are quite uniformly bluish-gray throughout the body, with certain exceptions in the males to be noted later. Emphasis has usually been laid on their distinctness from the black and the blue-splashed birds, but it seems important to note their resemblance to these two classes. In the first place, they are like the blacks in being *self*-colored, that is, all feathers in all parts of the body are pigmented. In the second they resemble the blue-splashed in that the color of the individual pigmented feathers is *blue* rather than black, save in certain sections of the males of both classes, where the feathers showing

pigment are a glossy black, apparently a secondary sexual characteristic. The blue appearance is due to the distribution and arrangement of the pigment granules in the feather structure, as will be described later. The fact that the splashed birds are splashed with blue (with the exception noted above) rather than black is important and appears not to have been noted, or at least not emphasized, by previous writers.

As an example, Punnett (1911, p. 70), in discussing the breeding behavior of the blue Andalusian, says: "It always throws 'wasters' of two kinds, viz., blacks, and whites *splashed with black*" (italics mine). In the material which has come under my observation, consisting of upwards of one hundred birds in the unrelated flocks of the poultry departments of Kansas State Agricultural College and the University of Wisconsin, no individual has been noted in which the pigmented areas were not distinctly bluish-gray, except that those pigmented feathers or parts of feathers appearing in the hackle, back, and saddle of the male were glossy black. These sections, it should be clearly understood, are also glossy black in the blue Andalusian male. There are occasionally flecks or small spots of black, appearing in the blue-gray feathers, and even in the white feathers of the blue-splashed birds. This is also true of the blues and, indeed, is not a rare occurrence in both dominant and recessive white races of other breeds. It does not in the least affect the fact that, in the material so far observed, the white birds have been splashed with bluish-gray rather than black in those sections where the blue Andalusian is also blue. This conclusion is borne out by the results of a microscopic examination.

In an effort to determine the fundamental differences between the three Andalusian phenotypes, a careful study of feathers from numerous individuals of each phenotype was made. A detailed account of the results of the study will be published in a later paper. For present purposes a short account of the most obvious differences will serve.

The pigment in all three phenotypes is black. The differences in appearance are due to the distribution and arrangement of the pigment or to its absence.

The pigment in a black Andalusian feather is in the form of rod-shaped granules, which almost completely fill each cell. They extend to the very tips of both curved and hooked barbules, and into the tiny hooklets given off from the barbs of the latter class. The cell boundaries are usually visible, due, apparently, to a slight contraction of the pigment, leaving very narrow pigment-free spaces between the cells. The former position of the nucleus of each cell is almost always plainly visible, due to an accumulation of pigment at its border, and to a narrow area surrounding it that bears relatively little pigment. In appearance, size and distribution the pigment granules in feathers from the black Langshan seem to be identical with those of black Andalusians.

The feathers from blue Andalusians differ from those of the blacks in two important particulars, namely, the restriction of the pigment in the feather structure and the shape of the granules. In blues of average shade, pigment fails to appear in the extremities of the barbules of both types. The hooklets are also entirely pigment-free. Though not always the case, the curved barbules usually carry rather more pigment than the hooked barbules, since the pigment extends further toward the distal end. As a usual thing that part of the hooked barbule which bears the hooks is free from pigment and does not differ in appearance, by transmitted light, from the same portion of a similar barbule from a white feather.

In the pigmented portions the pigment is usually markedly contracted or clumped within each cell, leaving a pigmentless space about the border much wider than is the case with blacks. These spaces are not always clean cut, but may be broken by invading rows of granules, or isolated granules may be found scattered within them. As a usual thing the nuclear boundaries in the cells of blue-gray feathers can only be made out with difficulty, if at all.

In cross-section, the pigment granules are seen to be scattered through the cortex of the barb and along the boundaries of the medullary cells. They are not restricted to the apex of the barb, as is reported by Lloyd-Jones (1915, p. 472, Figs. 37–39) in the so-called blue pigeon.

The predominating shape of the pigment granules in feathers from blue Andalusians is round. There may be a few elliptical granules and occasionally one which can not be classified otherwise than as a rod. These are quite rare, however, and one may carefully scrutinize several blue-gray feathers without finding any but round or very slightly elliptical granules. These round granules quite frequently appear in straight rows, giving the effect of a string of beads.

While the granule shape may have an appreciable effect in giving the bluish-gray cast found in blues and blue-splashed, it seems more likely that, as suggested above, the bluish appearance is due to the restriction or arrangement of the pigment. While the condition is not precisely the same as in pigeons, as described by Cole (1914, pp. 324–325) and Lloyd-Jones (1915, pp. 472–473), the optical effect appears to be from essentially the same causes, namely, the clumping of the pigment within the cells, and the reflection from this pigment through more or less transparent layers of keratin. It appears, however, that in the blue Andalusian the contrast between the pigment-free ends of the barbules and the pigmented barbs and barbule-bases is of more importance in producing the bluish effect than is suggested for the pigeon by these writers.

A characteristic of the typical blue Andalusian not before mentioned is that the contour feathers on the female and the breast feathers on the male present a laced appearance. This results from a black edging on that portion of each feather which is exposed when in its natural position. In this part of the feather the barbules on both sides of the barb are alike, being without hooks. The

cells in these barbules are more heavily pigmented than is true of the rest of the feather and the granules are rod shaped. In the regions where the black is giving way to blue, both round and rod-shaped granules are found.

All pigmented feathers secured from several blue-splashed females show identically the same pigment arrangement and granule shape as predominates in the blues. This holds true whether the portion examined comes from a feather that is pigmented throughout, or from one that is almost wholly white, with but a trace of pigment showing. In feathers which are pigmented throughout, the same relation regarding the lacing occurs as in homologous feathers in blue females.

The statements of the foregoing paragraph apply equally well to the feathers of those sections of the blue-splashed male which are blue in the blue male.

As previously mentioned, in both blue-splashed and blues, as well as in other self-colored races, black flecking or spotting not infrequently appears. Such spots, whether taken from a blue feather from a blue individual, or from a blue or an almost white feather from a blue-splashed bird, invariably show rod-shaped granules, while the surrounding area, if blue-gray, shows round granules. These spots are apparently entirely independent of the factors and conditions discussed in this paper and their appearance is comparatively limited. If hereditary, they probably depend on other factors. In handling blues and blue-splashed, however, one can not help being impressed with the possibility that these spots are caused by some interference with the full expression of the factors responsible for the arrangement and rounding of the pigment granules. Whether this interference is hereditary or environmental is as yet undetermined.

One further fact concerning the blue Andalusian males, already alluded to, is of interest. The long feathers of the neck (hackle) and saddle are glossy black. This is apparently a secondary sexual characteristic, though it is as yet undetermined whether it is due to the presence of

testicular secretion or the absence of ovarian secretion. The black feathers from both sections show rod-shaped granules predominating. There are numerous elliptical granules and a few round granules present. The pigment is not restricted as to distribution in the feather structure and is found even in the tiny hooklets of the hooked barbules, being in all these respects similar to the analogous feathers on a black male. These same conditions prevail in homologous pigmented feathers in a blue-splashed male.

The foregoing describes the conditions that usually prevail. There is some variation in all conditions described. In pure-bred blue Andalusians, for instance, there frequently appear areas that are not the usual clear blue-gray, but are dull and smoky. In such regions both round and rod-shaped granules are found in about equal numbers.

Bateson and Punnett (1906, p. 20) make note of the fact that the adult color of Andalusians may be determined from the down color of the young chicks. Examinations of the down show the same differences in granule shape that are observed in the adults. The blue and blue-splashed chicks for the most part show nothing but round granules in the down, while the blacks show rods.

It is of interest to note in this connection that a section from that portion of a barred Plymouth Rock feather where the black bar is giving way to the white, and the color is dull gray or dun with no bluish cast, there is a dilution of pigment as to amount, but no restriction as to arrangement or distribution. The pigment is fully extended through the barbule cells and consists of rod-shaped granules. There simply appears to be less pigment. While this is the usual condition, here, too, there is variation. At least one barred Rock individual was found whose feathers showed numerous round granules, though the rods predominated.

While it is generally accepted that blue Andalusians, when mated *inter se,* produce blacks, blues and blue-splashed in the ratio of 1 black to 2 blues to 1 blue-

splashed, exact data on this mating, as well as on the back crosses to black and blue-splashed, are really very meager. Bateson and Saunders (1902, p. 131) first suggested that the blue Andalusian was probably a heterozygote. Bateson and Punnett (1905, p. 118) quoted Mrs. Blacket Gill, a fancier of blue Andalusians, to the effect that blues mated to blues gave 22 blacks, 36 blues and 17 white-splashed (*i. e.*, blue-splashed). They secured stock from Mrs. Gill and made matings which gave the following results:

By the blue ♂ the white ♀ gave 34 blue, 20 white-splashed, and the black ♀ gave 27 blue, 19 black. In each case the result is qualitatively what would be expected if the blue is a heterozygote of *black* × *splashed white* [italics mine]; but whether the departure from equality indicates that some gametes bear the unsegregated blue, or may merely be taken as individual irregularities, can not yet be stated.

The same blue cock was bred with a black hen from Experiment 40 (in which the dark birds were unexpected), F_2, from White Wyandotte × Wh. Legh., giving as offspring 10 black, 15 slaty black to bluish. Hence, therefore, it is evident that the black ♀ was a homozygous black. The 10 blacks are the result of the union of the black gametes from the Andalusian ♂ with those of the ♀, and the 15 slaty resulted from the meeting of the black of the hen with the white-splashed from the Andalusian.

Bateson and Punnett (1906, p. 20) give the following summary of the data upon which the case of the blue Andalusian largely rests at the present time.

In Report I it was suggested that the blue colour of the Andalusian is probably heterozygous, and in Report II (p. 118) figures were given in support of this view. During the past two years additional evidence has been acquired, and every form of mating has now been tested, with the following results:

No. of Experiment	Nature of Mating	Result		
		Black	Blue	Wh. Spl.
Rep. II, p. 118	Blue ♀'s × blue ♂	22	36	17
Exp. 276	Blue ♀'s × blue ♂	19	42	22
(Total numbers for blue and blue		41	78	39)
[Expectation (inserted by the writer)		39.5	79	39.5]
Rep. II, p. 118	Wh. spl. ♀ × blue ♂	—	34	20
" " " "	Black ♀ × blue ♂	19	27	—
Exp. 269	Wh. spl. ♀'s × wh. spl. ♂	—	—	40
" 270	Black ♀ × wh. spl. ♂	—	20	—
" 294	Black ♀ × black ♂	25	—	—

The colour of most of the chickens was determined in the down. In the blacks the down is black with the exception of the ventral surface, the tips of the wings, and sometimes parts of the head, which are white. The down in the blues is slaty-blue, similarly marked with white, whilst in the white splashed it is of an exceedingly pale blue tint as a rule, though sometimes practically colourless.

The above figures bear out the view we previously expressed as to the heterozygous nature of the blues, . . .

The only other definite figures that have come under the writer's notice are from W. J. Coates, a blue Andalusian breeder of East Calais, Vermont, quoted by Platt (1916, p. 665) and referred to by Pearl (1917, p. 149). These are for matings of blue to blue and are as follows:

Mating	White (Blue-Splashed)	Blue	Black	Dark Red
A	4	10	3	1
B	4	5	2	0
C	3	3	0	3
D	0	12	1	0
E	3	3	1	0
	14	33	7	4

The fact that birds showing dark red appear is unusual and would seem to indicate that the Coates stock differs in its genetic constitution from the majority of the members of the breed, unless the occasional appearance of red is a fact usually suppressed by breeders.

Bateson and his co-workers make no attempt beyond that quoted above to account for the hereditary behavior of Andalusians and appear content to rest the case on the assumption that "blue is a heterozygote of black × splashed white."

The fact that "blue" is not a true intermediate between black and blue-splashed does not seem to have received due consideration. While the blue-gray bird is in a sense intermediate between self black and an individual that approaches white more or less closely, this intermediacy is more apparent than real. As previously pointed out, it is not intermediate in regard to either of the conditions involved when they are considered sepa-

rately. It resembles the black phenotype in being self-colored and the blue-splashed phenotype in having the pigment restriction within the barbules, which gives the blue-gray effect.

The 1:2:1 ratio may therefore be analyzed as follows:

Phenotypes	Pigment *not restricted* in barbule cells; *extended* through plumage ("self" condition); phenotype **black.**	Pigment *restricted* in barbule cells; *extended* through plumage (self); phenotype **blue.**	Pigment *restricted* in barbule cells; *not extended* through plumage; phenotype **blue-splashed.**
Ratio of phenotypes	1 :	2 :	1
Ratio for restriction in barbules	1 :	3	
Ratio for extension in plumage	3	:	1

In reality, then, the 1:2:1 ratio is the result of the combination of two 3:1 ratios.

The foregoing facts appear to lend themselves equally well to two interpretations. The first is that there are two pairs of allelomorphic factors at work. The second, that there is one pair of true allelomorphs (*i. e.*, factors having identical loci on homologous chromosomes), neither of which is recessive to the other in its manifestation in the phenotype.

The suggestion of two pairs of allelomorphic factors to explain the case of the Andalusian is not a new one. Goldschmidt (1913, p. 274) makes such a suggestion. After pointing out that the offspring of a pair of blues are black, blue, and "*schmutzigweiss*" in the ratio of 1:2:1, and that all three phenotypes carry pigment, he proposed two factors to account for the condition. The one is an "*Entfaltungsfaktor,*" which brings about a full development of the pigment. He represents this factor by "*Q*" (Quantität) which is possessed by the black race. The other factor, which is possessed by the "Weisse" race, he calls a "*Mosaikfaktor,*" which finely divides the pigment. This factor he designates *M* (Mosaik). He

finds it necessary to postulate further that Q is closely linked with m, and M is closely linked with q. Assuming pigment (P) to be present in all cases, he represents the "black" gamete as (mPQ), the "white" gamete as (MPq), and the F_1 blues as (mPQ)(MPq). The blue results from bringing M and Q into the same zygote. The monohybrid ratio results when the blues are inbred, however, because of the close coupling of the factors within the parentheses.

The Hagedoorns (1914, p. 179) also make use of two coupled factors in accounting for the hereditary behavior of blue Andalusians. They state:

> A blue Andalusian fowl, when mated by us to "recessive" white hens did not produce as many blue as white chicks, as should result on the hypothesis, that the white Andalusian is a recessive white (blue and black Andalusians being heterozygotes and homozygotes for one single genetic factor), but exclusively blacks and blues in equal proportions.

To account for this result they propose a gene A which is present in black Andalusians, but absent in the "white" Andalusian. The blacks, conversely, lack a gene B which is present in the "whites."

> This factor B, present in a pigmented fowl, actively "dilutes" the colour. It has no effect in the white Andalusians, because these, as they lack A, *are not pigmented* [italics mine]. We should therefore expect dilute black (blue) young from the cross black × white, which, inter se, would give AB, Ab, aB and ab offspring. Now, there is no evidence that in *Andalusians* there are ever produced $aabb$ animals, or $AABB$. There seems to be a mutual repulsion between A and B, so that no AB or ab gametes are ever produced. In some varieties of fowls this repulsion does not seem to exist, as pure strains of blue chickens occur.

Unless their material differs from any that has come under my observation the Hagedoorns err in assuming that what is frequently termed "the white Andalusian" carries no pigment, and Goldschmidt's suggestion accords more closely with the facts. Further, if the "recessive" white to which they refer was an Andalusian, the production of equal numbers of blues and blacks from a blue × white (blue-splashed) cross is difficult to understand. The expectation would be equal numbers of blue-splashed

and blues. If, as I suspect, the "recessive" white was a true recessive from another race, their results can only be interpreted by assuming that the "white" gametes as well as "black" gametes produced by the blue fowl carried a factor necessary for pigment production, which was lacking in the recessive whites.

If the latter is the case it accords with results I have obtained the past season. Among several matings made, preliminary to a further study of Andalusian blue, a white Wyandotte ♂ (*R 840* from the University of Wisconsin flock) was mated with blue-splashed Andalusian ♀♀ *M 409* and *M 539* (also kindly furnished by the poultry department of the University of Wisconsin). From *M 409* seven chicks were hatched, all of which were unmistakably bluish-gray. Six chicks which failed to hatch, but which did develop far enough for the color of the down to be determined, were also all blues. From *M 539,* brought in late in the season with the hope of increasing the numbers of chicks from this type of mating, three chicks were secured, which were again all bluish-gray. On the assumption that Wyandotte white is recessive (I am surprised to find no statement to this effect in the literature) these results would seem to indicate that a factor necessary for pigment formation as well as one causing the characteristic arrangement or restriction of the pigment found in blues, and both lacking in the Wyandotte, were furnished by the blue-splashed Andalusian. And further that a factor for the extension of this pigment to all feathers on the body was furnished by the Wyandotte. The blue offspring from this mating are assuredly not intermediates between a pure white parent and one that appears to be nearly white.

It is significant to note in this connection that the blue-gray offspring of the white Wyandotte × blue-splashed Andalusian cross show pigment granules that are predominatingly round. In some individuals they all appear to be round, while in others some rods may be made out. The down of black chicks, offspring of a blue Anda-

lusian ♂ and a white Plymouth Rock ♀, showed only rod-shaped granules. Feathers from a blue-gray individual, whose dam was a blue-splashed Andalusian and whose sire was a crossbred, the offspring of a Houdan ♂ × single-combed white Leghorn ♀ cross, showed only round granules.

If, as Goldschmidt assumes, his factors *mQ* and *Mq* are so closely linked that they never separate, and behave only as a single pair of factors, it is simpler to assume that there is but one pair of factors. As already pointed out, however, the discontinuity in the gradations from blue-splashed to black is such as to lead one strongly to suspect that two pairs of factors are at work. This discontinuity is greatly emphasized in the case of the blue offspring from the white Wyandotte × blue-splashed Andalusian cross. It is perhaps not impossible that a single pair of factors should bring about the result found in Andalusians, but it is so unusual as to make the assumption of two pairs of factors reasonable.

If this assumption is correct it must be further assumed, as Goldschmidt implies but does not state, that the black and splashed races each contribute a dominant and a recessive factor, and that in the blues we have the expression of both dominants, namely, the extension of pigment to all feathers, furnished by the black (or, in the Wyandotte cross noted above, by the white) parent, and the restriction of the pigment in the feather structure in such a way that the effect is bluish-gray, furnished by the blue-splashed parent. It is of interest in this connection to note that the blue condition produced by the restriction of the pigment in the barbule cells is recessive in pigeons (Cole, 1914, p. 325), while in Andalusians, on the above assumption, it is dominant.

While exact data concerning the breeding behavior of blue Andalusians are exceedingly meager, the experience of breeders generally seems to be in accord with such data as there are, and with the interpretation offered by Bateson and his associates. In order to account for the fail-

ure to secure a dihybrid ratio from the mating of blues, one is driven to assume linkage, and apparently a quite close linkage, of the dominant of one allelomorphic pair to the recessive of the other. As I hope to make clear, however, the linkage may not be complete, since it would easily be possible for crossing-over to occur occasionally with very slight likelihood of detection.

Goodale (1917, p. 213) has very recently shown that crossing-over occurs in the sex chromosome of the male fowl, though he has not as yet presented his evidence in detail. The universality of the laws of heredity throughout the plant and animal kingdoms is such that it would be a matter of surprise if crossing-over in fowls did not also occur in chromosomes other than the sex chromosome.

There is at present no certain criterion by which to predict whether, having assumed crossing-over in the autosomes of fowls, it occurs in one sex only or in both; and if in but one sex, which it may be, unless one chooses to suppose that it occurs only in the sex homozygous for the sex chromosome, as in Drosophila. If it occurs in both sexes, it is apparently so rare an event in Andalusians that the probability of securing two cross-over individuals in a mating made for purposes of analysis is so small as to be almost negligible.

After a somewhat extended microscopic study of blue-gray feathers from blues, blue-splashed and certain crosses, it seems more in accordance with their apparent action to refer to the factor responsible for changing black into bluish-gray as a restrictor, designated as R rather than M (Mosaikfactor) as was done by Goldschmidt. Similarly in place of Q (Quantität) I would suggest E, as responsible for the extension of pigment to all the feathers of the body.

Using this terminology and assuming for the moment complete linkage, a cross between individuals of the black and blue-splashed races, respectively, would appear as follows:

$$Er\ Er = \text{black} \times eR\ eR = \text{blue-splashed};$$

F_1 $$Er\ eR = \text{blue};$$

F_2 1 *Er Er* = black + 2 *Er eR* = blue + 1 *eR eR* = blue-splashed.

The gametes produced by the F_1 (blues) are *Er* and *eR*. If crossing-over should occur there would be occasional *ER* and *er* gametes produced. It is highly interesting to note that if these two classes of cross-over gametes were produced in equal numbers, as would be expected, and the individuals producing them were mated with ordinary blues, exactly the same phenotypic ratio would result as from the unions of the non-cross-over gametes, viz.:

F_1 crossover gametes	Ordinary gametes of F_1 blue
ER, *er*	*Er*, *eR*

F_2 *ER Er* = blue, *ER eR* = blue, *er Er* = black, *er eR* = blue-splashed.

This is the usual ratio of 1 black to 2 blues to 1 blue-splashed and would, from the very nature of the case, escape observation as involving crossing-over unless careful analysis were made of the hereditary constitution of these particular F_2 individuals.

Such analyses would not be impossible, though they might be long and tedious. The matings which would uncover any of the cross-over types, if offspring were produced in sufficient numbers to make it fairly certain that one were not dealing with chance variations in the ratios, are given herewith.

Cross-over blue of *ER Er* constitution mated with an ordinary blue would give the following expectation:

ER Er = blue cross-over × *Er eR* = ordinary blue;

F_1 *ER Er* = blue,
ER eR = blue,
Er Er = black,
Er eR = blue,

or 3 blues to 1 black, while the ordinary blues would give the normal 1 black to 2 blues to 1 blue-splashed.

Similarly this same individual mated with ordinary blue-splashed would produce all blues instead of the ordinary expectation of 1 blue to 1 blue-splashed, viz.:

$ER\ Er$ = blue cross-over $\times$ $eR\ eR$ = ordinary splashed;

F_1 $ER\ eR$ = blue,
$Er\ eR$ = blue.

If blue cross-over of the type $ER\ eR$ were mated with ordinary black the expectation would be all blues instead of the usual blues and blacks in equal numbers, viz.:

$ER\ eR$ = blue cross-over $\times$ $Er\ Er$ = black;

F_1 $ER\ Er$ = blue,
$eR\ Er$ = blue.

This second type of blue cross-over individual, $ER\ eR$, mated with ordinary blue, would give an expectation of 3 blues to 1 blue-splashed instead of the ordinary 1:2:1 ratio, viz.:

$ER\ eR$ = blue cross-over $\times$ $Er\ eR$ = ordinary blue;

F_1 $ER\ Er$ = blue,
$ER\ eR$ = blue,
$eR\ Er$ = blue,
$eR\ eR$ = blue-splashed.

If black cross-over $Er\ er$ were mated with ordinary blue the expectation would be 2 blacks to 1 blue to 1 blue-splashed instead of the ordinary ratio of equal numbers of blues and blacks, viz.:

$Er\ er$ = black cross-over $\times$ $Er\ eR$ = ordinary blue;

F_1 $Er\ Er$ = black,
$Er\ eR$ = blue,
$er\ Er$ = black,
$er\ eR$ = blue-splashed.

This same individual $Er\ er$ (black cross-over) mated with an ordinary splashed bird would give an expectation of half blues and half blue-splashed instead of all blues, as in the case of ordinary black and blue-splashed, viz.:

$Er\ er$ = black cross-over $\times$ $eR\ eR$ = ordinary blue-splashed;

F_1 $Er\ eR$ = blue,
$er\ eR$ = blue-splashed.

Finally, blue-splashed cross-over *eR er* mated with ordinary blue would give an expectation of 1 black to 1 blue to 2 blue-splashed instead of the ordinary expectation of equal numbers of blues and blue-splashed, viz.:

eR er = blue-splashed cross-over × *Er eR* = ordinary blue;

F_1

eR Er = blue,
eR eR = blue-splashed,
er Er = black,
er eR = blue-splashed.

The possible matings not indicated in the foregoing are those which would produce the same phenotypic ratios as if ordinary individuals (*i. e.*, non-cross-overs) of the same appearance as the cross-overs were used. Such matings are naturally of no value for analysis.

If it should later be shown that crossing-over does occur as suggested above and there are two pairs of factors concerned, there is the possibility of occasionally securing *ER* gametes. This in turn would seem to make possible the blue Andalusian breeder's long-time dream of producing blues that "breed true." With the appearance of the double recessive gamete *er* another race of Andalusian would apparently become possible, which, if the factors assumed in this paper are correct, should be white splashed with *black* instead of with blue.

The second possible interpretation of the facts so far established is that my postulated factors *R* and *E* occupy identical loci on homologous chromosomes, neither being recessive to the other in its phenotypic expression. For the present at least any evidence that this is the correct interpretation will be largely negative and come from continued failure to find cross-over individuals with regard to *R* and *E*. If these cross-overs should not be found it might at first appear that the interpretation of the case of the blue Andalusian is in all probability exactly what has been suggested from the first, namely, that blue is a heterozygote intermediate between the parental types.

Such an interpretation makes the characters *black* and *blue-splashed* the allelomorphs.

The practise of referring to *characters* that seem to behave in an alternative relationship in heredity as allelomorphs, instead of *factors occupying identical loci on homologous chromosomes,* is, it is to be hoped, passing. That it has lead to a misinterpretation in the present case is shown by the fact that all the offspring of certain pure white birds mated with blue-splashed ones are blue. The *E* factor must have come from an individual that was homozygous for it and devoid of pigment. It appears reasonable to expect that among the F_2's from the white Wyandotte $\times$ blue-splashed Andalusian cross will appear pure whites that carry the *R* factor. If this proves to be the case the allelomorphs are two factors, *R* and *E,* which act on black pigment. *R* arranges and restricts the pigment in the feather structure so that it gives a bluish-gray appearance. *E* extends any black pigment present to all the feathers of the body. One and probably either or both may be present without any phenotypic expression whatsoever. In fact, for every sixteen F_2 individuals from this cross four pure whites are to be expected in which the genotypic ratio with regard to *R* and *E* is 1 : 2 : 1, exactly as in the F_2's from a cross of a black and a blue-splashed Andalusian. One of these whites will be homozygous for *R* like the blue-splashed Andalusian. One will be homozygous for *E* like the black Andalusian. And two will be heterozygous for *E* and *R,* as are the blue Andalusians. But because there is no black pigment present these differences in the genotype do not affect the phenotype. For the sake of clearness the expectation of this cross is shown herewith, carried through the F_2 generation. *P* is taken to represent a factor necessary for the formation of pigment which is present in the blue-splashed Andalusian, but absent in the white Wyandotte, while *E* and *R* are represented as allelomorphic to each other.

White Wyandotte ♂ × blue-splashed Andalusian ♀.

	ppEE	*PPRR*		
F_1		*PpRE* = all blue;		
F_2	6 blues:	3 blue-splashed:	3 black:	4 white.
	2 *PPRE*	1 *PPRR*	1 *PPEE*	1 *ppRR*
	4 *PpRE*	2 *PpRR*	2 *PpEE*	2 *ppRE*
				1 *ppEE*

This same ratio (6:3:3:4), which is to be expected on either interpretation, has been reported by Baur (1914, p. 95) for crosses between a white-flowered race and certain plants bearing ivory-colored flowers, of the snapdragon (*Antirrhinum majus*).

Recessive mutations are of comparatively frequent occurrence. Dominant mutations, though much less frequent, have been described so often that they can not be reasonably doubted. There appears to be no reason, *a priori,* why a mutation might not occur where the mutated factors' potency of expression in the phenotype is approximately equal to that of the normal factor. That this has occurred, not once, but several times, might be the interpretation placed on the striking allelomorphic series reported by Nabours (1914, p. 141) for the color patterns of the grouse locust (*Paratettix*).

Upon which of the two alternative interpretations is correct appears to depend the possible success or the futility of the search for true breeding blues. The first makes it possible. The second appears to close the door of hope in the Andalusian breeder's face unless hope is seen in the progressive selection of the darker blue-splashed individuals. It does not appear possible, on the basis of present known facts, to reach a conclusion. Extensive matings are being made for the coming breeding season which it is hoped will throw further light on the matter.

Summary

1. This paper shows that blue Andalusians are like black Andalusians in that they are self-colored. They

are like the blue-splashed in that homologous pigmented feathers in both sexes have the same condition with reference to the restriction of pigment in the feather structure.

2. The fundamental phenotypic differences between black, blue and blue-splashed Andalusians are briefly described.

3. It is pointed out that the 1:2:1 ratio is in reality a combination of two 3:1 ratios.

4. The condition in the blues is shown to be due to the combined action of two factors *R* and *E*. *R* acts on black pigment, restricting its distribution in such a way that it gives the characteristic blue-gray appearance. *E* extends black pigment to every feather on the fowl's body.

5. It is impossible to decide on the basis of present facts whether *R* and *E* are located on identical loci of homologous chromosomes or are the dominants of two pairs of factors, each linked to the recessive allelomorph of the other.

6. It is shown that if the latter is the condition, crossing-over might occasionally occur between *R* and *E* with small likelihood of detection.[2] If crossing-over does occur, *RE* gametes are possible, which appears in turn to make possible true-breeding blues.

Acknowledgments

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[2] In ordinary practice poultry breeders make what are known as "pen matings," that is, one male is mated to a number of females and the offspring from these females are not kept separate. The exact parentage of any individual is therefore known only with regard to its sire, since its dam might be any one of the females in the group. As the detection of crossing-over depends upon the results of individual matings, it would be practically impossible to discover it under these conditions.

fessor Halpin very kindly placed stock and equipment at my disposal for an entire breeding season, without which it would not have been possible to carry on the breeding work reported herein.

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THE RÔLE OF FACTOR MUTATIONS IN EVOLUTION

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THE essential features of the mutation theory of evolution, as proposed by de Vries in 1901, are discontinuity and heritability of those variations which make evolution possible. New forms arise from preexisting forms by saltation; they occur in all directions; they are heritable; some of them are advantageous to the species and these are preserved by natural selection. These features are still recognized as the definitive elements of the mutation theory, but biologists are gradually changing their point of view concerning the *real nature of mutations themselves*. De Vries had worked with entire plants as units. He was searching for evidence of species in the making. He believed he had found this evidence when he discovered his new evening primroses at Hilversum and found that they transmitted their divergent characters to their progeny. The evidence appeared none the less clear to him, even though the parent species when tested did *not* always breed true, but continued to produce not only the forms first discovered, but also new ones which did not exist in the original population.

It is not my purpose to discuss the œnothera data which have accumulated in such enormous bulk in recent years. Goodspeed and Clausen, in their papers on species hybrids and the reaction-system concept of Mendelian heredity, have provided a strong argument for attributing many of the so-called mutations among the evening primroses to antecedent hybridization between distinct species. These authors have shown that "the occurrence of the 'mutants' (in *Œnothera*) and their subsequent behavior in hybridization admit of logical arrangement and inter-

pretation without any necessity for assumption of extensive germinal changes.'' On the other hand, Muller's recent investigation of balanced lethal factors in *Drosophila* led him to conclude ''that some (if not most) of the so-called mutations in *O. lamarckiana* are but the emergence into a state of homozygosis, through crossing over, of recessive factors constantly present in the heterozygous stock.'' If this is correct and these recessive characters arose as factor mutations, it is obvious that, in basing his theory of speciation by mutation on the evidence from Œnothera, de Vries builded better than he knew!

During the decade following de Vries's announcement of his theory biological interest shifted from the general problem of evolution to the more specific problem of heredity. The rediscovery of Mendel's law at once focused attention upon the inheritance of particular characters. Then began the era of experimental evolution in which, under the leadership of Morgan, most remarkable progress has already been made. The traditional problem of heredity, its mechanism, has been solved. We know, not only that the ultimate hereditary units are germinal, but also that they are located in that particular portion of the germ cell called the chromatin, and there is an ever-growing body of evidence proving that each hereditary unit occupies a particular locus in a particular chromosome. These hereditary units have been designated by various terms, but are most commonly referred to as genes, genetic factors, unit factors or simply factors.

The germ plasm has come to be recognized as an exceedingly complex stereochemic system, and, as Reichert has pointed out, on account of the impressionability and plasticity of such a system the germ plasm must be exceedingly sensitive to changes in internal and external conditions. That factors, however, are relatively stable entities is being clearly evidenced all the time. But occasionally they undergo definite alteration, doubtless as the natural result of some new or peculiar set of internal conditions. These alterations in genetic factors, or factor

mutations we shall call them, have been most thoroughly investigated in the common fruit fly, *Drosophila ampelophila,* in which species Morgan and others have discovered over 150 factor mutations, each of which is inherited in strict conformity with Mendel's laws, when tested in contrast with its normal mate as it exists in the wild type. This has become the classical evidence for the theory of factor mutations. Furthermore, it is now common practise to refer all Mendelizing characters to their hypothetical representatives in the germ cell, the genes or factors; and we speak of a pair of contrasted characters which are inherited according to Mendel's rule for the monohybrid as due to a single factor difference.

It is well known that Mendelizing characters exist generally throughout all groups of sexually reproduced organisms. Therefore it appears that factor mutations are of general occurrence. The data on factor differences will undoubtedly continue to increase in volume, and as they do our knowledge concerning the relative frequency of factor mutations will become more precise. In general Mendelian phenomena have been observed mostly in conspicuous characters, but certain minute character differences, such as forked bristles in *Drosophila* and size and shape of starch grains in peas, are inherited in Mendelian fashion. *Factor mutations, therefore, are sufficient to explain the origin of all differences between varieties, and doubtless they provide the necessary point of departure in the origin of new races.* If the new characters thus produced are beneficial or advantageous, then natural selection will cause them to be preserved. Sumner has recently discovered a number of interesting mutations in deer-mice (some as yet unpublished) and has shown that isolation may assist in differentiating local races. The writer is not unmindful of the earlier discussions of Wagner and others, and later of Jordan and others, on isolation as a cause of evolution. Many biologists are still inclined to think of geographical differences as the determinative condition in the production of new species. For

example, Harrison has discovered that certain species of moths, which are natives of different continents, but which resemble each other so closely morphologically as to be sometimes indistinguishable, exhibit extreme physiological differences. These physiological divergencies were indicated by the failure of hybridization between these species to produce offspring which were viable, or, if viable, which were fertile. Harrison concludes that geographical differences play a very important part in the production and accentuation of such physiological divergencies.

The rôle of the environment in the *production* of factor mutations is still an unsolved problem. As Caullery points out, the rôle of external factors in the production of mutations is no longer very clearly or directly apparent. It even appears that factor mutations occur in "all directions" quite independently of those elements of the environmental complex which are outside the organism. This does not mean that factor mutations are not caused. Like any other natural event, they must be dependent upon or conditioned by certain antecedent events, and, *a priori*, there is no reason why such antecedent events should not occur outside the organism. In other words, it is reasonable to suppose that specific elements of the external environment might induce permanent alterations in genetic factors. But, as yet, such a specific relation between the external environment and factor mutations can not be said to have been determined beyond reasonable doubt. On the other hand, migration, isolation and geographical differences along with other elements of the environment play an important rôle in the *selection* of mutations, and must, therefore, be recognized as of fundamental importance in organic evolution. It is conceivable, indeed, that, given the occurrence of factor mutations, the continuous impingement of some definite element in the environmental complex during long periods of time might condition a definite orthogenetic trend in phylogeny, as in the evolution of the elephant and the horse. But

may we safely assume the occurrence of the necessary factor mutations? The fact that such mutations are known in many species and that in *Drosophila* the same mutations have arisen anew in the same loci of homologous chromosomes of different pure strains would certainly indicate that we may. A factor mutation probably involves some sort of change within the group of similar molecules occupying a particular locus in a particular chromosome. Obviously the number and direction of the changes possible in such an entity are limited and the sum of the limits of change in all the loci in the chromosome group of a given species would define the limits of factor mutations for that species. The limits and direction of these mutations must have some bearing and may have intimate bearing upon orthogenetic trend.

Factor mutations produce new morphological and physiological characters such as distinguish the forms, races or varieties of existing species. As they occur generally in animals and plants at the present time, we may safely assume that they have occurred in preexisting organisms more or less frequently, and, therefore, that they have played a definite rôle in evolution. But just how extensive is this rôle? Can we account for the whole process of organic evolution including the origin not only of species, but also of genera, families, orders and phyla upon the basis of factor mutations? To be worthy of serious consideration a theory of evolution must account for the development of the organic world as we know it at present. Can the hypothesis of evolution through factor mutations fulfil this requirement?

It is well known that in many genera some of the species differ in their chromosome number. Do factors play a rôle in determining chromosome number? It is possible that they do. It is conceivable that a factor mutation might arise which would so alter the physico-chemical relations between different parts of the chromosome as to cause the chromosome to break at some point. Yet chromosomes are genetic units of a higher order than

factors, each chromosome containing many factors and in general behaving as a continuous entity. Glaser has recently suggested that while the chemical forces determining the specific structure of individual molecules may be precisely analogous to those which account for the nature of the hexose molecule, for example, yet aggregation into linear series in the case of the chromosomes very likely involves elements not strictly molecular. It seems to be necessary, therefore, to postulate some process by which these major entities become altered in number or recombined in entirely new systems. We are dealing here with phenomena of a different sort for factor mutations, and the latter appear, therefore, to be of slight significance in the origin of species having *unlike* chromosome numbers. Alterations in chromosome number may be brought about either by the unique or irregular behavior of one or more members of a chromosome group or by hybridization between species. Natural hybrids between distinct species of plants are of not infrequent occurrence and, according to Lotsy, species hybrids are known in the following groups of animals: Echinodermata, Vermes, Arthropoda, especially the insects, Mollusca, Amphibia, Aves in which even generic hybrids are known, and among mammals where there are several well-known cases of fertile hybrids. As for unique chromosome behavior, several different types have been discovered and are known to occur *occasionally.* Those which contribute directly to chromosome group evolution are: (*a*) non-disjunction of homologous chromosomes in the heterotypic or true reduction division, preceding gamete formation; (*b*) failure or retardation of the reduction division, resulting in chromosome groups of three, four or more times the haploid number of the parent species; (*c*) fragmentation or loss of one or more chromosomes, resulting in gross changes in the germinal reaction system and hence potentially in new species. The occurrence of the last type has not been proved, but, from his cytological investigations of several species of *Drosophila,* Metz in-

fers that within this group of species there has been a definite evolution of chromosome groups.

The known methods of species formation, therefore, may be described as follows: (1) Factor mutations, causing more or less extensive heritable somatic changes, some of which are adapted to the environment and persist. These, under the influence of natural selection, provide the means for gradual differentiation of groups having the same chromosome numbers. Presumably these groups would be recognized at successive stages in the process as geographical or ecological forms or races, distinct varieties and, ultimately, related species. (2) *Chromosome group alterations,* which produce new and sometimes inconstant forms, but which may also produce true species. (3) *Species crosses,* which are known to give rise to new types, some of them constant, but mostly inconstant forms, all of which are cryptomeres, potentially capable of throwing new combinations of parental characters indefinitely. The possibility should also be noted here that new constant types, having different numbers of chromosomes from the parent species, might originate as species hybrids.

Factor mutations occasionally produce new *dominant* characters. This fact, now fully established by various investigations, is of considerable theoretical significance. It has been a common practise during recent years to explain the origin of recessive characters as due to *verlust* mutations, *i. e.,* mutations due to the "loss" of factors. This conception has been associated with the much used though inadequate "presence and absence" hypothesis, according to which the only relations which can exist with respect to a certain factor depend on its presence or absence from the hereditary material. Difficulties are met when attempts are made to explain the origin of dominant mutations in terms of this hypothesis, for in such cases it is necessary to assume that a factor has been added to the hereditary material. As a result of employing the presence and absence hypothesis in genetic nomen-

clature we have the conception of evolution, recently suggested by Bateson and expanded by C. B. Davenport, which holds that "the foundation of the organic world was laid when a tremendously complex, vital molecule, capable of splitting up into a vast number of kinds of other vital molecules, was evolved," and that the process of evolution may be described as the unpacking of this "original package" by the process of loss of factors or portions of factors. Various lines of evidence indicate that changes in species are the result of some process of factor changes. But those who adopt a physico-chemical conception of factors and factor changes will find it unnecessary to imagine the "primordial amœba" in which was laid the foundation of the organic world as possessing in some mysteriously generalized condition all the genetic factors that comprise the hereditary complex of the genus *Homo,* since it is not by the "loss" or "fractionation" of factors that hereditary changes have been wrought. A gene does not "drop out" or "split up" into two or more —rather *a gene or factor is altered so that its reactions condition a different somatic end product.* It is not by loss of factors, but by changes in the composition of factors, supplemented by intercrossing, that new races, new varieties, and new species having the same chromosome number, originate.

Definite organization of the "hereditary substance par excellence," the chromatin, probably occurred in certain prototypes of existing organisms, in which the chromatic substance was not differentiated from the remainder of the cell plasm. The recent papers of Minchin on the evolution of the cell and of Troland on the enzyme theory of life show that the most probable early course of evolution was from that unorganized state typical of the Chlamydozoa, which are supposed to consist of free chromatin material, up through advancing degrees of differentiation between the specialized hereditary substance and the remainder of the protoplast. Between this fairly satisfactory conception of the earliest steps in evolution and the ever-

strengthening evidence that factor mutations furnish the means for evolutionary change within existing species, it must be admitted that there is a wide gap which needs to be filled. May we not look to future studies on the phylogeny of the chromosomes to supply this need in some measure? I venture to suggest that more work like that of Metz on the chromosome groups of related species will prove to be an important source of further light on this problem.

We may now consider the rôle of factor mutations in more detail. It is certain that even those species having the same chromosome number differ as a rule in many unit factors. Hence in order to explain the origin of one from the other it is necessary to assume one of three possible methods of procedure.

1. There may have been one or more *factor mutations having manifold somatic effects.* That profound somatic differences such as would distinguish species from one another are sometimes produced by single factor mutations is proved by the results of the crosses between the oak-like walnut and its parent, the California black walnut, which I have described in earlier papers. The mutant form, unlike most so-called monophyllous varieties, differs from its parent in every gross external feature, yet it behaves as a simple recessive in F_1 and F_2. However, *factor mutations which induce such extensive somatic changes seem to be exceedingly rare.*

2. There may have been *simultaneous mutations in several factors,* thus producing full-fledged an individual of a new species. Objection to this hypothesis is found in the observation that factor mutations always or nearly always occur singly, *i. e.,* a single factor mutation in a given individual at a given time. This observation is mathematically predictable since the probability of the occurrence of two factor mutations in the same individual at the same time, according to the principle of least squares, would be the inverse ratio of the square of the number of typical (unchanged) individuals in the popu-

lation. Thus, for example, if one factor mutation occurs in one individual among say 1,000, then the probability of two factor mutations occurring in the same individual at the same time would be once in 1,000,000 times. Moreover, individuals showing even one factor mutation are comparatively rare. Hence, *it appears extremely doubtful that any species have arisen through simultaneous factor mutations in single individuals.*

3. *Single factor mutations may have occurred in different individuals within a group either simultaneously or successively.* This hypothesis implies that individuals possessing certain mutant characters are capable of maintaining themselves in the wild state, an assumption which is justified by the fact that factor mutations are known which have not impaired vitality and fertility, nor reduced the general adaptability of the organism. Further evidence to support this hypothesis is found in the widespread existence of composite species. Although these heterogeneous groups have been classified as species, they are really aggregates of numerous distinct varieties or subspecies. Indeed, their Mendelian behavior indicates that many advantageous physiological characters, such as earliness or lateness of maturity, resistance to disease, high fecundity or possession of a certain pigment, originate through factor mutations. Such mutations frequently, though not necessarily, involve morphological changes also. In all except strictly autogenous (self-fertilized) species new combinations of mutant characters would occur through intercrossing, thus increasing the chances of beneficial or advantageous results to the species. Populations of such species consist of individuals of heterogeneous germinal constitution, and frequently disadvantageous or even lethal factor mutations persist in heterozygous condition, but soon make their presence manifest when inbreeding or self-fertilization is practised. Autogenous species, on the other hand, are composed of individuals of homogeneous germinal constitution (pure lines) which have arisen through the re-

currence of factor mutations. When in a certain germ cell of such an individual a mutation occurs which will produce a detrimental or lethal effect, the offspring will either die or fail to reproduce as the case may be. Hence pure lines possess no lethal or highly detrimental factors; yet these biotypes may vary between wide limits in their morphological and physiological characters.

There is no necessity whatever for the simultaneous appearance of mutations in order to establish new forms. Only three conditions are necessary in this method of evolution: the existence of species during long periods of time; repeated occurrence of some factor mutations resulting in new characters advantageous to the species; and the transmission of these mutations from generation to generation. All these conditions are known to exist. In fact, the repeated occurrence of the same mutation in the same locus of a particular chromosome has been observed, as well as the occurrence of different factor mutations producing similar somatic variations.

Factor mutations, therefore, provide the means for gradual evolution within species; only a few, to be sure, out of many factor mutations being preserved, but these few being sufficient, with the frequent aid of migration or isolation by geographical barriers, to build up new groups which can be recognized only as distinct species. But these new species, it will be understood, would have the same chromosome numbers as the ones from which they arose. We are, therefore, considering here only one of several methods by which new species originate. Strictly speaking, the only true mutations are factor mutations, as they are the only known germinal variations.

Conclusion

Factor mutations occur in accordance with the general scheme of the mutation theory as formulated by de Vries. They arise suddenly, they occur in all directions, they are heritable, and some of them are advantageous to the species and are preserved by natural selection. When so

preserved they give rise to new forms or races, and when fostered by man they make possible new horticultural varieties of plants or new breeds of animals. It is probable, as Morgan has shown, that factor mutations alone have furnished the necessary germinal changes to make possible the evolution of the elephant's trunk and similar cases of orthogenetic development which have been discovered by paleontologists. But factor mutations alone are not sufficient, so far as we know, to account for the origin of species of different chromosome numbers, much less for the appearance of phyla and genera. It is to be hoped that light will be shed on these more obscure phases of the general problem of organic evolution through a combination of taxonomic, genetic, cytological and physiological researches. It would seem that the solution must involve the expression of relationships between organic groups in terms of the morphology and physiology of the chromosomes.

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PHYSIOLOGICAL PROBLEMS IN THE LIFE-HISTORIES OF ANIMALS WITH PARTICULAR REFERENCE TO THEIR SEASONAL APPEARANCE[1]

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I. INTRODUCTION

THE fact that plants flower, fruits ripen, insects appear and disappear in succession throughout a growing season needs no statement even to the savage huntsman or the city flat dweller. The variations of the usual succession of appearances with peculiar seasons, unusual weather, etc., are general guides to many operations of primitive agriculture and matters of comment by all out of door people. Seasonal succession has long been scientifically investigated (see Alee, '11; Forbes, '16; Harvey, '08; Hough, '64; Johnstone, '08; Shelford, '13). Only recently has careful investigation of it been stimulated by the general interest in modern ecology and economic problems. The importance of a knowledge of delayed germination of seeds to the agriculturist (Crocker, '06) has further stimulated work along a line throwing light on the general subject. The analysis of the physiological causes of the normal succession of biological events in any season calls on many of the laws of biology to formulate merely the outline or even a portion of a life history, as, *e. g.*, the answers to questions such as why potato beetles appear from hibernation at a certain time, and not earlier, and deposit eggs on plants of the genus *Solanum*. Further, as soon as we concern ourselves with the analysis of the causes of the irregularities of appearance in any season, the evident complication of problems is such that one may

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undertake to discuss them without apology. The practical significance of variations to agriculture is shown by the destruction of the wheat crop in the Southwest by the wheat aphis. This was due to differences in response to weather on the part of the pest as compared with its enemies. The cause of seasonal appearance, or more especially of variations of seasonal appearance, is to be found in the influence of external factors on the initiation and velocity of growth and on fecundity and length of life, in dormancy in various stages in the life histories, and in the adjustment of the innate rhythm to the annual climatic cycle.

II. The Influence of External Conditions on Time of Appearance and Number of Individuals

1. *Differences in Initiation and Velocity of Development.*—The problem of initiation of development is one that has attracted much attention of late on account of the importance of an ability to predict the time when various insect pests will emerge from hibernation or will reach a stage of development at which it is necessary to spray, if such treatment is to prove satisfactory.

In this connection attention has been directed to the conditions, particularly of temperature, under which there is no development during periods lying within the bounds of the ordinary life history of the animal in question (Sanderson, '10, Headlee, and Peairs). The limit at which development does not take place, usually called physiological zero or zero of development, is better termed *threshold of development*. Sanderson has discussed various data and theories relative to the effect of temperature on development.

The attention of physiologists has been directed toward the study of the effects of temperature on the rate of metabolism and development. In general the results of such study have been interpreted with reference to Van't Hoff's law relative to the increase of reaction with a rise of temperature of 10 degrees, usually des-

ignated as Q_{10}. Vt is the velocity of development at any temperature (t), so that Q_{10} is the quotient of $\frac{V(t+01)}{Vt}$ and supposedly is a constant. In fact, the Q_{10} is not a constant for living phenomena, but usually varies from 2 to 3, being greater for the lower temperatures and smaller for the higher ones. Snyder has pointed out in detail that while the temperature coefficient for differences of 10 degrees varies, the variation is not only for physiological actions, but also for many chemical reactions; in both cases the variations are in the same direction. He finds that changes in viscosity with changes in temperature follow the same rule. He holds the hypothesis that even in the simpler physiological actions we have to deal with at least two distinct chemical actions whose fundamental velocities at any given temperature are different.

Recently Krogh ('14) has calculated the Q_{10} from Q_1, Q_2 and the like, at different temperatures for the time from fertilization of the frog's egg to the appearance of the first cleavage plane. He found 53.0 (published as 5.3, which appears to be a error) for the interval between 3 and 5 degrees, 4.1 for the interval 5 to 10 degrees, 2.0 for the interval 15 to 20 degrees. He raises the question as to the value of such a variable "constant." He calls attention to the fact that the velocity curve (the reciprocal of the time-temperature curve) is a straight line within certain limits. This is not the curve for the reciprocal of Van't Hoff's time and temperature formula. The latter law is valuable only as evidence that the life process is a combination of chemical processes. The condition of any environmental factor at which development does not take place, but immediately above which development may be initiated, is called the *threshold of development.* It is evident that there is a threshold of development for most species as regards temperature, moisture, light, oxygen, quantity and quality of food, and probably other factors. The brief state-

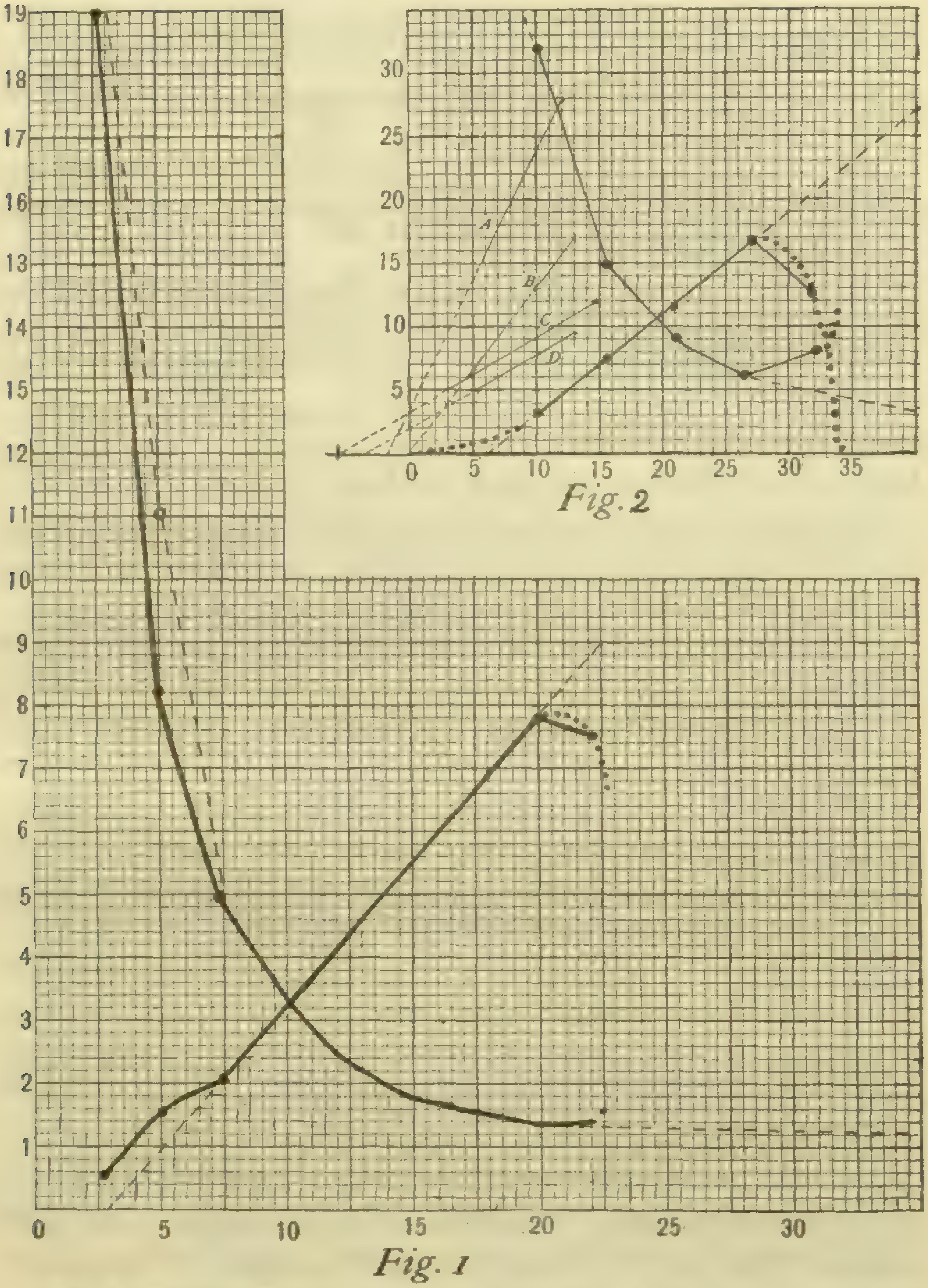

Fig. 2

Fig. 1

FIG. 1. Showing the time-temperature curve (the longer curve) for the appearance of the first cleavage plane in the egg of the frog. The solid curved line is the actual curve, and the broken line extensions are theoretical, based on the thermal constant (time × temperature) where it differs from the actual one. The shorter oblique curve is the velocity curve, or the reciprocal of the time-temperature curve, shown for the true hyperbola by the combined broken and solid lines of the longer curve. It is a straight line. The line of heavy dots shows the probable continuation of the curve based on Verworn's ('99, p. 397) irritability curve. The figures on the axis of abscissas are degrees Centigrade. The figures on the ordinates represent 100 minutes for the hyperbola and 100 divided by the time units for the reciprocal (from data by Krogh).

FIG. 2. Showing the time-temperature and velocity curves for the time from

ments and citations below are in support of this statement.

(*a*) *Temperature Threshold*

Very nearly at the time of the publication of Krogh's work, Sanderson and Peairs announced that for a large series of insects the time-temperature curve for development is a hyperbola and the velocity of development curve is a straight line. Peairs concluded further that the (reciprocal) relative velocity curve which is obtained by dividing unity (100 to avoid fractions) by the experimentally determined time periods, in days or other units, and plotting it against the temperature for which the time was observed, gives points for the different temperatures which fall in a straight line crossing the axis of temperature at the *zero* of the curve, or the theoretical threshold of development (Fig. 1). This theoretical threshold may be calculated also with two points accurately determined experimentally. These authors conclude that with the zero determined, the thermal constant (temperature multiplied by time—a constant for an hyperbola) can be obtained. However, they failed to note the deviations from law which occur at both high and low temperatures and which require careful attention in practical work.

These entomological workers appear to have overlooked the work of the fish culturists who have studied the subject of effects of temperature on development. Apstein ('11), Dannevig ('94), Earll ('78), Green ('70), Johansen and Krogh ('14), Reibisch ('02), and Williamson ('08) all made contributions of greater or less importance. All called attention to the effect of tempera-

birth to maturity of *Toxoptera graminum* (from Headlee after Sanderson and Peairs); the velocity curve represented by a heavy line is extended with dots to show the usual form of the irritability curve, and its mathematic extensions are shown as a heavy broken line. The light oblique lines are the velocity curves for the development of the eggs of four species of marine fish (after Krogh). *A*, the flounder (*Pleuronectes flesus*); *B*, the whiting (*Gadus merlangus*); *C*, the cod (*Gadus morrhua*); *D*, the plaice (*Pleuronectes platessa*). It will be noted that the mathematical zeros of development as indicated are at or below zero Centigrade and the rate of increase in development for each degree of rise of temperature is different for the different species and is indicated by the angle which the velocity curves make with the axes of the curves. The figures on the axis of abscissas represent degrees Centigrade. The figures on the axis of ordinates are days for the hyperbola and 100 divided by days for its reciprocal.

ture on the rate of fish development, particularly during the late embryonic stages. Reibisch ('02) showed that time × temperature is a constant, using the hyperbola. He called the temperature at which development could be initiated by the slightest increase the "*threshold temperature,*" which is the same as the zero of development and physiological zero of other authors. He calculated this from the hyperbola formula, thus anticipating the work of Sanderson and Peairs by about eleven years. In fact, the idea of ineffective temperature below a minimum and a sum of temperatures which is the product of time × temperature dates from de Candolle's 1830 article.

Johansen and Krogh worked over the data of Dannevig and showed that the velocity is different for different fishes (Fig. 2, *A, B, C*). They note further that temperature is not absorbed by the organism and that the constant is only a convenience. They call attention to the fact that the velocity-of-development curve is a straight line which, prolonged downward, crosses the axis of abscissas at a point mathematically corresponding to Reibisch's threshold temperature. The threshold of development would be where the velocity curve crosses the axis of abscissas if the straight-line velocity curve held good and the time-temperature curve were a true hyperbola. Krogh ('14) showed that while 2.7 degrees is the mathematical threshold of development for cleavage of the frog's egg, the first cleavage appeared at this temperature 1,844 minutes after fertilization. If the curve were an hyperbola, at 2.7 degrees the development of the cleavage plane should have required an indefinitely long time; or, in other words, it should not have appeared at all. Also, at 4.9 degrees the appearance of the cleavage plane should have required 1,100 minutes, while the observed time was approximately 730 minutes. Further, it required 138 minutes for the cleavage furrow to appear at 22.1 degrees, which is more than at 20.7 degrees, showing a decrease in velocity at higher temperatures. Thus Krogh points out that the velocity curve is a straight line only between 7

and 21 degrees, while the limit of development is from less than 3 to 22.1.

Thus comparing the velocity curves for Headlee's development of Toxoptera (Fig. 1) and for the cleavage of the frog's egg, we note that in the case of the frog's egg the velocity is too great at the lower temperatures and falls off at the highest temperature. Also, in the case of Headlee's curve for Toxoptera, the development was much too slow at the higher temperatures. Krogh ('14) further studied the development of pupæ of *Tenebrio molitor,* carefully measuring the carbon dioxide given off. He found that the curve of velocity was a straight line between 18.5 and 28 degrees, but that it curved upward at lower temperatures. He tried incubating the pupæ at 13.45 degrees, which is the mathematical zero of his curve, and found that they developed in 1,116 hours, but with considerable mortality. At approximately 33 degrees the velocity was less than it should be if the curve were a true hyperbola. An interesting feature of these curves is that they approach so nearly to the curve published by Verworn showing the stimulation effect of heat on activity. This curve is shown in Fig. 2 by the actual velocity curve and the dotted extensions which, when compared with the curve of Krogh for the development of *Strongylocentrotus, Arbacia,* and *Tenebrio,* indicate the close relation between the amount and rate of activity and that of general metabolism and growth.

Edwards ('02) made a careful study of the hen's egg and established 20–21° C. as the point at which no development takes place. There is an optimum temperature and development is accelerated by slightly higher temperatures and retarded by lower temperatures. Thus even in a warm-blooded species there is a point at and below which development does not occur.

(*b*) *Prediction on the Basis of Temperature Laws*

Can we predict the time of appearance of any stage in the life cycle of an animal? Certainly, in so far as we

are concerned only with temperature and with temperatures within the straight-line limits of the velocity curve, we can predict with a high degree of accuracy the time at which any stage will be reached. Further, within the

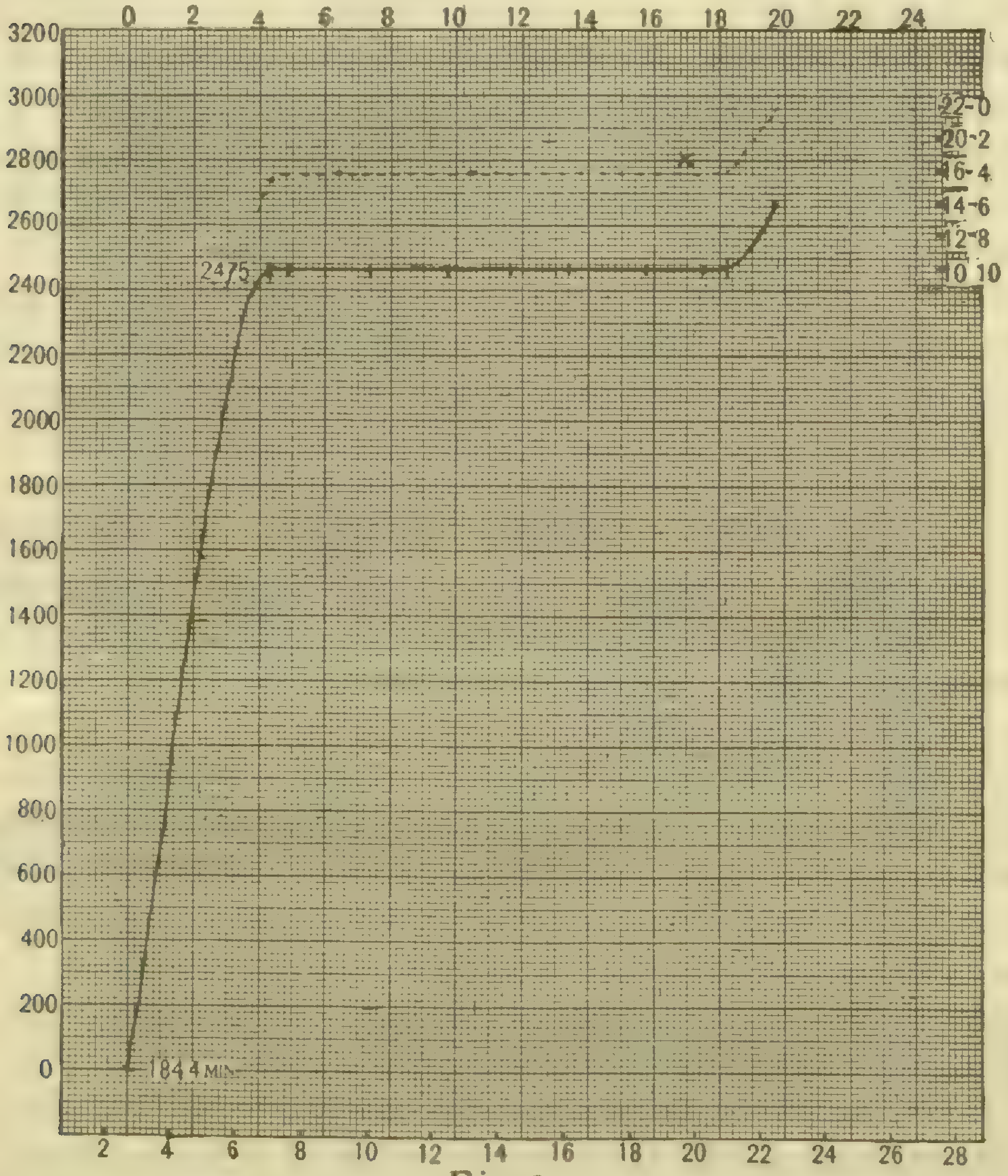

Fig. 3

FIG. 3. Showing the total temperature curve for the appearance of the first cleavage furrow in the egg of the European frog, as a continuous line from the data of Krogh. The small cross dashes show the temperature at which experiments were performed. The actual temperatures are given at the bottom of figure; at the top the actual degrees above the theoretical threshold of development, which is 2.7 degrees C. The figures at the left show the total minute-degrees, time × temperature, which range from zero on the scale to 3200. At the right is shown a scale for different degrees of light; these figures are added to illustrate a method of chart-making only. 10 units of light are assumed to give quickest development, and both increases and decreases, to give slower development and hence more time-temperature units, as suggested by the broken line above the main curve. The cross shows approximately what the total time-temperature would be if darkness slowed the formation of the cleavage furrow in the same manner as it slowed general development during an entire month in the experiments of Yung. For further explanation see text.

straight-line limits the effects of constant and variable temperatures should be the same. This is due to the fact that the product of time units × temperature above the threshold of development is a constant within the straight line limits. Where it is not a constant, the actual values may be plotted approximately for any temperature.

Using the data of Krogh (Fig. 3), I have drawn an approximate total temperature curve for the development of the first cleavage plane for the egg of the frog. The number of degree-minutes required for completion of the cleavage furrow is the same for all temperatures between 7° and 21° C. That is time × temperature is constant between 7° and 21° C., where it is about 2,475 time-temperature units or minute-degrees, and the curve is a straight line. Above 21 degrees the total temperature is greater than the constant, and below the lower limit of the constant it is less than the constant. At 2.7 degrees it should be infinity if the hyperbola held good, but is actually 1,844 minutes. The time-temperature units are not expressible at this point, so the actual time is given. If development takes place below the zero of the hyperbola, the time-temperature units may be considered as having a negative value, but are expressible. From this curve it is possible to tell how long it takes for the cleavage furrow to develop at any temperature shown; for example, take 6 degrees (bottom of chart = 3.3 degrees at top). We find from the curve that the total temperature for this is approximately 2,200 degree-minutes. Thus, 2,200 divided by 6.0 − 2.7 gives 666 minutes. It is true that the same result could be obtained by reading off the time on a time-temperature curve (near to hyperbola) with less labor, but the region in which the total temperature is a constant cannot be shown on such a curve; and the time for different temperatures is obtained with less simple calculations from the reciprocal. The total temperature curve exaggerates the straight-line limits, and brings out sharply the fact that high temperatures retard and low temperatures accelerate as compared with the veloci-

ties indicated by the reciprocal of the hyperbola to which the data partially conform.

Factors other than temperature influence the rate of development. The work of Yung showed that in the case of the frog light is one of these. Unfortunately the light was not measured definitely in the work of either Krogh or Yung. Yung kept one lot of developing frogs in the dark and one in a window but where the sun actually never shone on them. Krogh's work must have been done in similar light. Yung's larvæ were reared under the light conditions which he used, for a month or two months, and thus his data are for older stages than those of Krogh, whose results relate to the appearance of the first cleavage furrow. Accordingly, any comparison of the two sets of data is essentially impossible. However, for the purpose of illustrating a principle which is indicated relative to development under the influence of various intensities of factors other than temperature, I have called the light condition under which Krogh's work was done 10 units and have shown it on a scale at the right-hand side of the graph. It is probable that too strong light will retard development as well as too weak light. Hence the scale is shown double, 12–8, 14–6, etc.; either increases or decreases in light intensity are assumed to increase the time required for development. The cross shown on the graph gives the approximate total temperature for darkness indicated by Yung's work. This part of the chart is given merely to indicate a method of chart making—of showing the way in which variations of one other factor change the number of time-temperature units required for development.

For practical prediction such a curve must be drawn for the shortest time for development at each temperature. This will be under optimum light, chemical, etc., conditions for the temperature concerned. In establishing such a least-total temperature curve a few careful determinations within the straight-line limits with other factors optimum will suffice. Outside these limits the de-

terminations must be more numerous and especial care must be exercised to have the temperatures constant. In determining the optimum light for different temperature much more rapid progress can be made by running experiments under at least three conditions of this factor for each temperature. Deviations due to factors other than temperature should be shown on such a chart probably in a manner indicated by the broken line on Fig. 3. If the main curve is drawn for shortest time, all deviations in light, etc., will *increase* the so-called total temperature, and lines may be drawn for these conditions above the main curve as the facts necessitate.

Much investigation will be necessary to determine the corrections which must be made in determining *mean* temperatures which must be derived from conditions in which the temperature slowly rises and falls during several hours of each day, within the ranges of temperature where the velocity curve is not a straight line. Temperatures outside the straight-line limits should not be mixed with the temperatures of the straight line limits. These outside temperatures must be considered or estimated in terms of units sufficiently small to approach accuracy. In the case of daily temperature fluctuations the temperatures outside the straight-line limits must be considered by hours, and suitable corrections made before they can be included in the daily mean. The exact nature of this correction will have to be determined by careful investigation.

(*d*) *Humidity Threshold*

The workers thus far cited have studied temperature alone, intending in a general way to keep other factors constant. There is undoubtedly a threshold of development with reference to each factor which influences development. Berger found that growth ceased in tenebrionid larvæ fed on bran dried at 105 degrees, and that they lived for months with a loss of weight; doubtless with a very small increase in moisture they could be maintained at the initial weight. More recently Pierce has found

that the cotton boll-weevil has a different zero or threshold of development and different temperature optimum for each humidity.

(*e*) *Oxygen Threshold*

The development of various invertebrates is stopped by insufficient oxygen (Loeb, '06, and citations). Johansen and Krogh found that if the oxygen pressure was reduced to one half by reducing the air pressure to 380 mm. of mercury development of plaice eggs was retarded. The oxygen pressure threshold of development lies below the amount which will go into solution from air at pressure of 230 mm. of mercury, but at this concentration much care was necessary to keep the eggs alive. Shull ('11) determined the oxygen minimum for the germination of the seeds of *Xanthium.*

(*f*) *Light Threshold*

Loeb ('11) states further that light is necessary to the regeneration of zoids in *Eudendrium.* Its absence is further known to slow development in larvæ of insects which normally live in the light (Bachmetjew, 692). Smith found that light accelerates the development of salmon. Johansen and Krogh found little difference between marine fishes grown in light or in dark. Davenport ('99) summarized the literature to that date and showed on the authority of Yung that moderately strong light increased growth.

(*g*) *Food Threshold*

Recent work has shown that food may be either qualitatively or quantitatively deficient and cause standstill in the development of mammals. Thus Osborne and Mendel (p. 101) show the following methods of producing it:

(1) By under-feeding with rations of suitable qualitative make-up; (2) by the use of diets containing an adequate protein but with inorganic salts supplied in the form of a mixture of pure chemicals together with sucrose and starch as the carbohydrate component; (3) by restricting

the protein content of the dietary below the minimum required for growth; (4) by furnishing as the exclusive source of nitrogenous intake proteins which lack some amino-acid group indispensable to growth.

Thus the animals were maintained at practically the same weight and they retained their power to grow long past the age at which growth normally ceases (335 days) and for periods equal to half the normal life of the species, which is 1,000 days.

Wodsedalek ('17) has shown that certain tenebrionid larvæ can not only be maintained, but may be reduced from half-grown to hatching size several times by repeated starving and feeding. This seems to leave little doubt as to the existence of a threshold of development for food.

(*h*) *Definite Amount of Development*

Krogh has shown that the total amount of carbon dioxide given off by pupæ of *Tenebrio molitor* is the same for all temperatures, showing that there is a definite amount of development to be attained. The rate appears to be different for different species where no considerable difference in the total for passing the stage in question is to be expected, as in the case of fishes (see graphs by Krogh). Thus, difference in velocity and increase in velocity at different temperatures and moistures, etc., have an important bearing on the variable or unequal seasonal appearance of the different species. The acceleration of development under conditions of factors near the threshold is a further consideration (for a noteworthy instance see Bachmetjew's ('07) retabulation of Merrifeld's ('90) data) which leads to non-coincident appearance and peculiar modification of normal sequence in abnormal seasons.

It appears that the chief reason that there are not more generations in an annual cycle in the case of spiders or other animals is that the amount of energy which must be expended and the velocity of development are such

that the completed sexually mature individual can not be produced oftener than usually obtains. There is, to be sure, much evidence that the tendency to hibernate is not very firmly established in some species and that under stimulation animals may be induced to reproduce nearly continuously, at least for a number of generations. Cessation of development in any given case is as much attributable to some factor falling below the threshold of development as to heredity. The environment is extremely complex, and the number of factors which may cause cessation of development and which have been already established, are so numerous as to indicate that the number is very much greater than is commonly supposed, including temperature, moisture, light, oxygen, evaporation, quantity of food, or absence of any one of many necessary food constituents. These appear to operate in accordance with the law of toleration (Shelford, '13) and, with respect to food, in accord with Leibig's law of minimum. Where dormant periods are well established, their occurrence with reference to the usual seasonal rhythm makes any modification of the usual life history difficult or impossible.

Variations from the "normal" seasonal weather, and weather changes are of especial interest as modifying the usual seasonal succession of adult animals or any area. In springs with unusually prolonged cool weather, the various pond species, such, for example, as those noted on page 146, are crowded together, and reach maturity much more nearly at the same time than in normal seasons. The same phenomenon has been observed by the writer in the case of the flowering of early spring plants of an area near Chicago. The differences in the response of different species to the same conditions show their different physiological constitutions. This type of variation indicates that such maladjustments as resulted in the depletion of the grain crop by the grain aphis in the southern part of the wheat belt, because the weather favored them, may occur in undisturbed localities, though

probably not to the same degree. Seasonal succession and its variation involve, for the pure-science student, many of the problems which confront the economic zoologist.

3. *Length of Life and Fecundity.*—One phenomenon which has been repeatedly noted in connection with this study—a matter of common observation—is the variation in numbers of individuals in different years. The length of life of individuals may have a pronounced effect on the population and succession of species on a given area. Loeb has stated that the great number of individuals in the plankton of the polar seas in summer is due to the longer life of the individual at low temperature. Unless the low temperature slows the different processes unequally this can hardly follow. For example, if a parthenogenetic female aphid normally lives a week and produces 1,000 offspring and then the temperature is lowered so as to prolong the life to three weeks, unless the different functions were unequally affected by the change, there would be at the end of three weeks but a thousand, while at the normal rate there would have been a billion possible individuals. On the other hand, if the rate of reproduction remains the same and the length of life of the individual after the reproductive period is increased, the results of lower temperature would be very different, perhaps much as Loeb assumes. Actual observations along this line are few. In the case of the San José scale, however, Glenn ('15) found that the number of offspring is greatest in the individuals breeding in the warmest weather. Turning to Table I we note (page 146) that *Agelena nevea* may live longer in the adult stage than *Argiope aurantia,* or the time of appearance may be more irregular, and hence the question is one for investigation.

The velocity of development of different species is different, and the relative velocity is measurable in some terms of the angle which the velocity curve makes with the axis of abscissas (Fig. 2). Thus when we compare the four species of fish given by Dannevig we note that

velocity of development increases more rapidly with increases of temperature for the flounder than for the plaice; the same difference exists between the whiting and the cod. Krogh showed that the velocities of the different stages of the frog's egg, Fig. 1, are the same; but the different stages in the life history of the same animal may differ in velocity at the same temperature.

4. *Dormancy.*—Dormancy is of much importance among animals inhabiting the same area. Thus the eggs of *Eubranchipus* and *Diaptomus stagnalis* require both summer drying and winter freezing before they will hatch. Dormancy is common in the eggs of grasshoppers (Thomas, '79), walking sticks (Trouvelot), etc. Dormant periods are common, occurring even in deer and armadillo embryos (Patterson), and probably represent hereditary remnants of impressions made on former generations by seasonal rhythms.

The causes of these rhythms often are simple. Concerning delayed germination or dormancy of seeds, Crocker and Davis ('14) have said:

> The work to date has shown that delayed germination of seeds is secured in a variety of ways: by almost absolute exclusion of water by seed coats (as in the hard-seeded legumes and species of several other families), by the limiting of the degree of swelling of the embryo, . . . by reduction of oxygen supply below the minimum for germination . . .; and finally perhaps by deficiency in salts. To this must be added delays due to embryo characters.

Dormancy has been overcome by drying in the case of several species of insects in the writer's laboratory.

III. Seasonal Succession as Illustrated by the Spiders of a Small Area of Ground

In the spring and summer of 1910, Mr. G. D. Allen undertook the study of the seasonal succession of the fauna of an area in a vacant lot at Eighty-first Street and Blackstone Avenue, Chicago, which is a pond in spring and low prairie in summer, but did not complete the work, though his collections were extensive and thorough, extending

from the middle of June to November. Miss Katherine Norcross arranged the records in seasonal order, except those of the spiders. In the case of the insects which made up the vast majority of species on such an area, the question constantly arose as to where the insect had been previous to its appearance there. During the spring and summer of 1913, the writer undertook to collect and observe the spiders of the plot studied by Allen. Spiders were selected for this study because they do not undergo a metamorphosis, and may often be found and identified in a juvenile condition while insects can not. Though incomplete, the data are adequate for a discussion of the physiological features of seasonal succession.

The habitat from which the specimens were collected was about 25 × 50 ft., nearly all of it covered with water in early spring, usually drying during May, and containing water thereafter only during and after especially heavy rains. In July Allen found the vegetation composed chiefly of *Eleocharis, Spartina, Carex, Juncus, Liatris, Steironema, Cacalia,* and several other composites. The plants taken together made up what is commonly called coarse grass and weeds. The writer's collections in 1913 were made on or very near Allen's dates for 1910. From these joint sources the data of the following table were obtained and arranged, but with some gaps where the spiders were probably too young to identify. The records marked "*C*" are taken from Comstock ('11) and represent the conditions in which the spiders usually are at the dates indicated. The spiders were identified by Banks ('10) and the nomenclature is according to his list.

1. *Statement of Succession.*—In the spring the area is a pond in which various Crustacea and worms succeed each other (see Shelford, '13, pp. 278). Sexually mature adults appeared in abundance about as follows: *Amblystoma tigrinum,* March 15; *Eubranchipus,* April 15; *Planaria velata,* May 1; *Diaptomus stagnalis,* May 1. Some of these animals have been studied sufficiently to show that they become dormant for the remainder of the year

as soon as the pond dries up. *Amblystoma tigrinum* deposits its eggs and then burrows into the mud and remains ten months in estivation and hibernation. *Eubranchipus* deposits eggs that must be both dried and frozen before hatching. *Diaptomus stagnalis* is similar in character. *Planaria velata* forms cysts which live over to the following spring.

TABLE I

SHOWING SEASONAL SUCCESSION OF ADULT SPIDERS ON A LOW PRAIRIE SUMMER DRY POND

The species are arranged in the order of the seasonal occurrence of adults. * indicates adults; *j*, young; *e*, eggs; *g*, generic identification only. *C* indicates that the occurrence is creditable to Comstock and is not based upon the author's observation. Dates are given at the heads of the columns in numerals only.

	4–20	5–6	5–22	5–26	7–10	7–24	8–6	9–6	9–30	10–12	11–6	Adult Weight in Gs.
	1	2	3	4	5	6	7	8	9	10	11	
Pardosa modica Blck.	*	*	*									
Tetragnatha laboriosa Htz.	*gj*	*	...	*	...	**j*	*	*j*	...	*j*	...	.....
Xysticus gulosus Key	*gj*	*	...	...	...	...	...	*	*	*j*	*j*	.....
Dictyna sublata Htz.	...	*	*	*	...	*j*	*j*	*j*	*j*	*j*	...	.....
Pisaurina undata Htz.	...	*	...	...	...	**j*	**j*	*j*	*j*	*j*	...	300
Attus palustris Peck	...	*	...	*	...	...	*	...	...	...	...	.....
Pardosa canadensis Blck.	*gj*	*j*	*j*	*	*	...	...	...	...	...	...	.....
Lycosa heluo Wal.	...	...	...	*	*	...	...	*	...	...	...	.....
Phidippus podagrosus Htz.	*j*	*j*	*j*	**j*	*	*	*j*	*j*	...	*j*	...	200
Plectana stellata Htz.	...	...	...	**j*	...	...	*	...	*	...	...	25
Epeira trivittata Key	...	...	...	...	*	...	*	*	...	...	...	.....
Runcinia aleatoria Htz.	...	...	...	...	*j*	*	*	...	...	...	...	160
Mangora gibberosa Htz.	...	...	...	...	...	**C*	*	...	...	...	...	.....
Agelena nivėa Wal.	...	...	*jC*	*j*	*j*	*	*	*	*	*	*eC*	80
Misumessus asperatus Htz.	...	...	...	*j*	*j*	*j*	**j*	...	...	...	...	.....
Phidippus audax Htz.	*jC*	*jC*	*jC*	*jC*	*jC*	*jC*	*	**j*	**jC*	*jC*	*jC*	80
Argiope aurantia Luc.	*jC*	*jC*	*jC*	*jC*	*jC*	*jC*	*	*	*	*jC*	*jC*	.....
Argiope trifasciata Forsk.	*jC*	*jC*	*j*	*j*	*j*	*j*	*	*	*	*eC*	*jC*	425

At the time these appear, land animals begin to move about the pond margin, adult and juvenile spiders among them. The collection and arrangement of the entire fauna showed the same thing as the spiders, but proved much less satisfactory in the other cases than was expected, owing to a lack of knowledge of life histories and an inability to identify young stages. Turning to Table I and following out the stars which indicate the occur-

rence of adults, and noting that the species have been arranged in the seasonal order, starting with *Pardosa modica* Beck, which was taken only in April, we end the season with adult *Argiope trifasciata,* which appeared as adults late in the season only.

We note that when the collection proved at all complete the juvenile individuals follow the adults of the early spring species, and that they both precede and follow the species which mature late in the season. The collections proved to have been made with insufficient detail, and many young spiders could be identified only to the genus and are usually omitted entirely. However, the tables show a sufficient general arrangement of the species throughout a season to furnish an adequate basis for a discussion of the problems involved in the phenomenon of seasonal succession—the problems presented by a comparison of the few species whose life histories are known quite completely.

IV. Discussion

Nearly all species are adjusted to the seasonal rhythm of the habitat in which they live. Thus *Dyctina sublata* appears as adult in May and June, when, as it seems, eggs must be laid, and juvenile forms characterize the late summer and autumn. *Argiope trifasciata* deposit eggs in October and passes the winter in the juvenile form. *Phidippus podagrosus* reaches maturity in July, when eggs must be deposited, and young occur in both fall and spring. These differences generally represent an innate adjustment of the life cycle to seasonal rhythm, not readily broken up. It is to be expected, then, that *Dictyna* will deposit eggs to better advantage and that the young hatch better in May than in November, as is the case of *Agelena nivea.* It is further to be expected that the young stages of some spiders will not go on with development until cooled for a considerable period. Perhaps one of the most interesting questions concerning the whole matter of succession of spiders is to be found in the fact that from what is known about them, they are all active

for about the same period of time; *i. e.*, all life histories involve about the same period of activity and rest.

An inspection of the table shows that the time of reaching the adult stage varies for the different species, so that there is a general change of spiders in the adult stage as the season progresses. This is all that seasonal succession can mean under any conditions; the fact that the eggs or other young stages can not be identified or their location is unknown does not change the character of phenomenon in any locality where the species are resident.

The causes of the succession of species may be roughly summarized as follows: Species differ in the time in the annual climatic rhythm at which development begins, in the time of occurrence of dormancy and in the conditions necessary to break it up, in threshold of development relative to several climatic factors, in velocity of development relative to several climatic factors, food, etc., and in size and total energy expended. These may be taken up one at a time.

Considering differences in the time in the annual cycle at which development begins, as a factor in seasonal succession, we must notice first that this can be a controlling factor only where there is no dormancy in the life history or where the available total of temperature, moisture, light, etc., above the thresholds is just enough to produce one generation per year and not to permit of a gradual moving of the time of appearance to an earlier date each season, during several successive long seasons. The test of this would come in the migration of agricultural pests which are arrivals in localities where the growing season is longer. There appear to be no easily available facts, and for the present this type of maintaining a definite time of appearance is to be regarded as a theoretical possibility. The fact that the life histories of various animals which have been known to migrate extensively into new territory appear not to be accelerated indicates that dormancy may control appearance and thus time of beginning development may be a secondary consideration.

Thus we come to the time of occurrence of dormancy and the conditions necessary to break it up, which result in the rhythmic tendency of the species fitting into the rhythm of the climate in which it lives. In many insect species it appears that drying may be substituted for freezing. Such species may migrate into climates in which there is a dry season, instead of a cold one, and with a longer growing season, and continue with the usual annual life-history rhythm. Under these conditions in each growing season the development is stopped by dormancy and proceeds no further until the drying breaks up dormancy. The development of *Eubranchipus,* once initiated, proceeds until the mature individual has produced eggs. Here dormancy stops all further progress until the eggs are first dried and then frozen and warmed above 0° C. Crustacea without dormant periods go on developing and produce several generations in one summer. After the conditions necessary for the overcoming of the dormancy have been fulfilled, or where there is no dormancy, species differ in the threshold conditions for development. The thresholds for development are hardly the same for any two species in which thresholds have been determined. Thus species will differ in the time at which development is initiated in the spring. Further, the increase in velocity with increase in temperature is different for different species, as indicated by the differences in the angle which their velocity curves make with the axis of abscissas (see Krogh, '14, velocity curves of several species of fish, also Fig. 2). This fact alone makes it possible for a given set of conditions out of the ordinary to give a peculiar and irregular occurrence of the different species of a community.

The total energy as illustrated by the CO_2 given off by a species is the same for all conditions in which development can occur at all, as shown by Krogh. It is probable, accordingly, that the total energy expended in development is different for each different species. This may bear some relation to size and weight, though alcoholic

specimens of full-grown females of several species of spiders were weighed and no conclusion could be drawn. Either the method of obtaining the data or the fact that the spiders are all annual is the cause. Krogh found that the velocity of development is the same at the same temperature in the different stages of the frog, though the thresholds are different. But there is no reason to assume that this is true of other animals, especially where there is a metamorphosis.

1. *Conclusions.*—The preceding pages indicate the intricacy of the problems involved in explaining the simplest life history of annual animals. The physiological life histories of animals which have two or more generations per year, and of those whose life cycle extends over more than one year, are still more difficult to deal with. The problems involved have of late attracted the interest of biologists generally, of geneticists, of economic entomologists, of fish culturists, and others, and they constitute a central group of problems for the ecologist. All these various interests are being focused on the problems of physiological life histories as the next step in the attempt to advance the science of biology. In all these lines, the day of the naturalist taxonomist as a central figure is all but past, and the day of the naturalist physiologist is at hand.

This interest has arisen in the various groups for different causes, but one of them is the variation which occurs in the succession of species and their interaction in different years, due to peculiar weather conditions. The green bugs destroyed the wheat crop in 1907 because of differences in thresholds of development of the aphid pests and their enemies; the fruit growers do not spray at the right time in many cases because the insect pests do not appear at the usual time. This is not to be credited to the effects of one factor alone; as, for example, enough work with temperature has been done to show that, while it is important, the influence of other factors is sufficient to make prediction on the basis of temperature alone quite unreliable.

The animal geographer is interested in the same problems. We note that the animal community illustrated by the spiders contained animals maturing at every season of the year. There is a noticeable early spring or vernal group which the geographer has assumed is montane in origin (Adams, '09); and the group of land species which appears through the summer is traced into different situations according to specific affinities. It is evident that successful species are those that fit into the seasonal rhythm with respect to physical conditions, food, and numerous other relations.

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THE USES OF INSECT GALLS

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Introduction

This paper, which is a contribution from the Branch of Forest Insects, Bureau of Entomology, is a summary of an extensive study of the literature dealing with the uses of insect galls. It was made primarily to obtain a history of the use of the Aleppo gall in the dyeing industry. In the preparation of this paper I have been assisted by Mr. S. A. Rohwer under whose direction the research of the literature was made.

For centuries before the real origin of insect galls was known, they were noted and given a place, like most other vegetable substances, among remedies for diseases. The ignorance of their origin gave rise to queer superstitions and practises even among scholars, especially in the Middle Ages, when they were gravely recorded as supernatural growths and employed as a means of foretelling the events of the coming year. The gall was supposed to contain a maggot, a fly, or a spider, each of which betokened some misfortune. If the inhabitant were a maggot the coming year would bring famine, if a fly, war, or if a spider, pestilence. This belief was recorded and practised for several centuries, even after the time of Malpighi, who was the first in the Western World to discover and make known the true origin of insect galls.

The record of the practical use of galls has come down from the old physicians and naturalists of Greece and Rome. Their observations were confined chiefly to the Aleppo gall and the Bedeguar of the rose, but an interesting statement is found concerning two galls which were used by the Greeks to burn without oil in their lamps.

These were *Cynips theophrastea* and an undetermined gall called by Pliny the black gall-nut.

Until very recently in all histories of drugs, tanning, and dyeing, galls have been considered as of great importance, and at the present time are among the most valued ingredients of ink. The first use of galls was in medicine and many besides those discussed below have been listed as drugs.

Among the Cynipids is the gall of field cirsium produced by *Cynips* species (determined by Cuvier) which was formerly considered, if merely carried in the pocket, as a very efficacious remedy for hemorrhages. Others merely mentioned are (*Cynips quercus-terminalis*) = *Biorhiza pallida, Cynips polycera, Cynips quercus-tozæ, Dryophanta quercus-folii, Andricus fœcundatrix,* and the undetermined galls called by Guibort, *galle corniculée, galle marmorine,* and *galle d'Istrie.* This last, according to Trimble, yields 24 per cent. tannic acid.

Besides the Cynipid galls there is a gall on *Pistachia khinjuk,* called Gúl-i-pista, produced by *Pemphigus pallidus,* which enters into the materia medica of India. Two other Indian galls used in medicine are found on *Tamarix.* One, called Bara-Mai, occurs on *Tamarix galica,* and the other, Chota-Mai, occurs on *Tamarix orientalis.* Another *Tamarix* gall said to have been used by the Egyptians in medicine is one called by them Chersamel, and by the Turks, according to Fockeu, Bazgendge.

To the Cynipids useful in tanning Kieffer has added *Cynips lignicola* and *Cynips hungarica;* and to those used in dyeing, (*Cynips tinctoria-nostra*) = *Cynips infectoria* Hartig. *Cynips quercus-petioli* Linnæus, according to the *Gardeners' Chronicle,* 1854, is also capable of forming a strong black dye.

Burton in his journeys in East Africa noted a gall-nut which was used by the Somali women as the basis of their tattooing dye. This gall has not been determined, but the record is of interest as being the only one encountered of a savage people's making use of galls.

Another undetermined gall is that called by Pomet "Bazdyendge" and described by him as a reddish gall on a species of oak in Turkey, which was used with cochineal and tartar to make a very fine scarlet.

So far as can be ascertained no American galls were ever used for any practical purpose by the Indian (statement of Dr. Hough, U. S. National Museum), and but few by the white man. No interest appears to have been taken in this phase of gall history in America until Trimble, through his interest in the history of tannins, took up the question of tannic acid in galls and analyzed a few North American galls. He found that many of these galls contained relatively large amounts of tannin. He stated that there are more oaks in the United States than in Europe which are available for tanning, and that as the gall partakes of the character of its host-plant then there must necessarily be more oak galls in this country suitable for tanning. He also remarks that it is not known that all species of oak yield the same tannin, therefore we may look for a variation in the properties and composition of the tannins from different species.

Of the Cynipid galls examined by Trimble the richest in tannin is one from Texas, on *Quercus virens,* closely resembling the Aleppo gall and containing 40 per cent. tannic acid. This has been identified by Mr. S. A. Rohwer as *Disholcaspis cinerosa. Acraspis erinacei* (determined by L. O. Howard) was found to contain 17.89 per cent. tannic acid and *Disholcaspis globulus* Fitch, 3.91 per cent.

A Dipterous gall on *Quercus alba,* determined by L. O. Howard as *Cecidomyia* or *Diplosis* species, contains, according to Trimble, 9.24 per cent. tannic when air-dried, and 31.68 per cent. when quickly dried by artificial heat at 80 degrees.

A gall occurring on *Rhus glabra,* in many ways the counterpart of the Chinese gall, was found by Trimble to yield, when air-dried, 61.70 per cent. tannic acid which is about 8.3 per cent. less than the Chinese galls yield and about 3 per cent. less than the Aleppo. This has been

identified by Mr. A. C. Baker as *Melaphis rhois* Fitch.

Besides the American galls suggested by Trimble as being of possible use in the industries, a few have been recorded as food.

The galls of *Disholcaspis weldi* (Beutenmüller) which occur on *Quercus reticulata* in Mexico were purchased at a fruit stand in Mexico City.

Oak-apple galls produced by *Cynips* spp. are eaten by school children, and some of them are said to be sweeter than sugar.

The most important record on the use of American galls is a note by Dr. A. D. Hopkins on a black oak gall produced possibly by *Callirhytis* sp. This gall, because of its resemblance to wheat, is called "black oak wheat" and "wheat mass" (typographical error for mast[1]). Specimens of this gall were received from Westcott, Mo., with the information that they were very abundant and had been fed to cattle, hogs, sheep, turkeys and chickens all of which were fond of them and were getting fat on them. These galls were also received from Texarkana, Ark., where they were used to fatten hogs.

The following food analysis and report were made on these galls in the old Dendro-Chemical Laboratory, Bureau of Chemistry, U. S. Department of Agriculture, under the direction of the late Dr. W. H. Krug:

	Per Cent.
Moisture	12.24
Ether extract	3.37
Crude fiber (indigestible)	9.34
Protein	8.56
Ash	2.89
Carbohydrates (starch, etc.)	63.60
Relative food value = 93.43	
Nutritive ratio = 8.4	

The relative food value is high and the nutritive ratio is wide, showing that this material is especially adapted for fattening animals.

[1] Mast is used for nuts collectively, acorns, chestnuts, beechnuts, etc., especially when used as food for hogs and other animals.

CYNIPS GALLÆ-TINCTORIÆ Olivier

The gall of *Cynips gallæ-tinctoriæ* Olivier, known in commerce as the Aleppo gall, Turkey gall, Levant gall, gall-nut, gall of commerce and ink marble, is found in eastern Europe, that is, in Hungary, Turkey and Greece, and in western Asia, on *Quercus ægilops, Quercus infectoria, Quercus pedunculata* and possibly *Quercus humilis.* This gall as an article of commerce has had the longest history, having been used from the time of the ancient Greeks to the present; has been used for the greatest variety of purposes; and has been considered as the richest of all the galls known to the Western World.

Medicine.—The earliest use of this gall was in medicine in which capacity it was known to the Greeks and to the Romans. In Greece it was recorded as of medical value by Hippocrates in the fifth century B.C. and then by Theophrastus, third century B.C. Its use by the Romans was treated at some length by Pliny, who stated that twenty-three remedies were compounded of gall-nuts, and that among the diseases for which they were used were ulcerations of the mouth, affections of the gums and uvula, malformed nails, hang nails, etc., and that for the relief of toothache and burns the inner part of the gall should be chewed.

From these early days until very recent times authors of Materia Medica have included this gall-nut as a drug, designating it as "the most powerful of vegetable stringents." In modern times it has been used in Europe as a cure for fevers and was especially popular in France early in the eighteenth century. At that time Poupart in *Mem. Ac. Sci.,* 1702, made a report on it which proved it to be of doubtful efficacy. Nevertheless its use was continued and as late as 1849 Pereira, in London, listed it as useful for medical purposes, recommending it as a tonic in intermittents, an astringent in hemorrhages, a chemical antidote, a topical astringent and giving a list of six medicines concocted from it. At the present time gall

products are found in the British Pharmacopœia as astringent ointments and in the U. S. Pharmacopœia, 1916, ninth revision, the Aleppo gall still appears as the source of tannic acid and as the principal ingredient in the preparation *Unguentum gallæ*. It is now used only externally.

Ink.—In the manufacture of ink the Aleppo gall was long considered as a necessary ingredient, especially where a durable ink was required, as in court records. In some places the law required that records be made with ink compounded of gall-nuts.

This use of the gall is not of such ancient origin as the medical use, for Pliny, who quotes the older authorities on other matters, has made mention only of the ink compounded of lampblack, which was used also by the Chinese. Hoefer in his "Histoire de la Chimie" spoke of an ink used in the third and fourth centuries A.D., compounded of acid and metal solution but failed to say that this acid was obtained from gall-nuts. The ink made from gall apple was, however, well known to the monks of the ninth and tenth centuries, who used it in copying their manuscripts. An interesting reference to the ink made from gall-nuts occurs in Scheffel's "Ekkehard," a romance of the tenth century, in which the monk Ekkehard says ". . . all ink comes from gall apples and all gall apples from a wicked wasp's sting." Of course, this is of interest only if the knowledge of the origin of the gall apple were part of the experience of the tenth-century monk and not supplied from the knowledge of the nineteenth-century author. As the search to clear up this point would be long and arduous and the result of no real value it has not been made.

From the ninth century down to the present day, gall-nuts have been included in practically every good ink recipe for black writing and record inks. The Aleppo gall is considered as the best for ink-making, but other important ones are the Morea gall, the Smyrna gall, Marmora gall and Istrian gall, and other good quality galls

from France, Hungary, Italy, Senegal and Barbary. The Chinese and Japanese galls are also sometimes mentioned in recipes. The Japanese gall has been used in making school and other cheap inks.

The Massachusetts Record Commission in 1891 made a Report on Record Inks and Paper in which the superiority of gall-nut ink was attested. The ink made from gall-nuts was said to be permanent, if properly made, and to have the advantage that if the writing should fade it could be repeatedly restored by a solution of nut-gall or tannin. Any other coloring matter substituted in whole or in part for gall-nut and iron solution impairs the quality of the ink.

In 1912, Oyster in the "Spatula Ink Formulary" gives as the basis of the best black writing and record inks, gall-nuts. In the recipes for inks used by the United States Treasury, Bank of England, the German Chancellory, and the Danish Government the Aleppo gall is specified.

Lehnen also states that nut-gall extract forms an excellent material for the preparation of ink, especially where manufacturers can not keep large stocks of the nut-gall itself. According to the 1917 annual report of the *Oil, Paint and Drug Reporter,* large quantities of gall-nut extracts are imported into the United States. Of course, all of it may not be used for ink manufacture.

Tanning.—Among tanning materials this gall-nut is the richest of all in the tanning principle and has been used, for tanning purposes, in the preparation of hides and skins, but because of its expense and its value to the textile colorist it has not been extensively used. Experiments and analyses of these galls were undertaken, however, with a view to discovering the tanning principle in vegetable matter. Pliny mentioned the preparation of leather as being one of the uses of gall-nuts, Bosc recorded galls as being used in the tanning of hides and Davis in 1897 spoke of them as being the richest in tannin of all tanning materials, but made no further mention of

them in his descriptions of the processes of tanning. Other more recent writers on tanning materials have also listed oak galls,

Dyeing.—In the history of the art of dyeing, the Aleppo gall figures largely from the earliest mention of the art in literature up to the very present. According to Theophrastus it was used by the Greeks in dyeing wool and woolen goods and Pliny mentioned it as being used to stain the hair black and as the best adapted for the preparation of leather and the dyeing of skins. As the ancients could not conceive of a scholar's taking an active interest in the technical arts there is no record of how these galls were used, merely the statements that they were so used; and it was not until the end of the eighteenth century that any definite knowledge of these galls was sought.

It was at that time, when science invaded nearly every field of endeavor, that the chemists made an earnest effort to determine the chemical contents and action of gall-nuts, so as to place the arts of dyeing and tanning on a firmer and more scientific basis. Déyeux in 1793 was the first to separate the tannin in the gall-nuts and his experiments were followed up by Scheele, to whom is accredited the discovery of gallic acid. Berthollet and Fourcroy made more detailed analyses of the gall-nuts and gave more positive knowledge of the various properties and their chemical value.

Berthollet in "The Elements of the Art of Dyeing" gave perhaps the first scientific account of the art of dyeing with full explanations of methods and materials. According to his idea the great value of the Aleppo gall lay in its astringency and as it is most astringent before the insect escapes, the immature galls, or as they are called, the blue galls, are of the most value and are the ones used in dyeing black, while the white galls, or those from which the insect has escaped, are used in dyeing light linens. For the dyeing of black Berthollet considered that no

other astringent than an infusion of gall-nuts could be used in the dyeing bath, as too large a quantity of any other material would be necessary to obtain the same results.

Bancroft, however, in his "Philosophy of Permanent Color," 1813, opposed the idea that the astringency was the important property of the gall-nut and set forth the idea that it should be considered merely as a coloring matter. In defense of his theory he showed that tannin procured from different vegetable matter and combined with iron will not produce black, and gallic acid alone will not blacken solutions of iron, while either tannin or gallic acid from *galls* combined with iron forms a black dye or ink.

At the present time both these theories are known to be true for the Aleppo gall may be used as a fixing agent in dyeing or may be used as the basis of a good black dye. As a dye its use appears to be confined to the dyeing of leather and of sealskin fur.

In the dyeing of leathers and skins the Aleppo gall is used in small quantities with other dyeing materials to obtain the best and most permanent black. That the successful dyeing of leathers, however, is not dependent entirely upon a good dye is evident from the following statement on leather dyeing by Bennett, "Manufacture of Leather," 1909:

> The absorption of the dye by the fiber has been considered a case of chemical action, of physical action and even as a case of "solid solution," but it is highly probable that more than one type of action comes into play and that possibly all these theories may be true to a certain extent. It would, however, appear that with vegetable tannages the determining factor is the formation of color lakes with the tannin on the fiber. The tannins are of an acid nature and fix the basic dyes with great readiness, but the basic chrome-tanned leathers fix the basic dyes much less readily than the acid dyes, so it is clear that the nature of the tannage has considerable influence in the matter.

For the dressing and dyeing of sealskin furs, large quantities of the Aleppo galls were formerly shipped to

London, where all of our American sealskins were dressed and dyed for the market. Now, however, this industry has been established in the United States, and in 1914 gall-nuts worth $17,174 were imported from Bagdad for this purpose. As the method of dyeing sealskins is a very jealously guarded trade secret the American firm engaged in this enterprise has had to work out its own processes, and according to the Commerce Reports this has been successfully accomplished and one sale of American sealskins dressed and dyed in America has taken place, in St. Louis, in September, 1916.

Analysis.—A gall so widely known and of such great value has of course been analyzed many times and is the standard for the analysis of others. According to Trimble the most generally accepted analysis is that made by Guibort, which is as follows:

	Per Cent.
Tannic acid	65
Gallic acid	2
Ellagic acid; Luteo-gallic acid	2
Chlorophyll and volatile oil	0.7
Brown extractive matter	2.5
Gum	2.5
Starch	2
Woody fiber	10.5
Sugar; Albumen; Potassium sulphate; Potassium gallate; Gallate of lime; Oxalate of lime; Phosphate	1.3
Moisture	11.5
	100.00

CYNIPS INSANA Westwood

A gall somewhat resembling the Aleppo gall and often confused with it is that produced by *Cynips insana* Westwood. It is better known as the mad apple of Sodom, Dead Sea fruit, or Mecca or Bussorah gall, and is found in Palestine, Asia Minor, Albania and Italy on *Quercus*

infectoria, *Quercus tauricola* and *Quercus farnetto* (*conferta*). Its use is confined to the locality from which it takes one of its names, Bussorah or Basra.

This gall has furnished an interesting and somewhat mystifying theme to poets and has been often discussed by old writers who have tried to connect this so-called fruit with some of the unknown fruits mentioned in the Bible.

In Bussorah or Basra in Asia Minor, probably its native heath, this gall is used by the inhabitants in dyeing Turkey red, and it is more esteemed by them than the Aleppo gall.

Analysis.—The following analysis of this gall was made by Bley in 1853:

	Per Cent.
Tannic acid	26.00
Gallic acid	1.60
Fatty oil	0.60
Resin	3.40
Extractive and salts	2.00
Starch	8.40
Woody fiber	46.00
Moisture	12.00
	100.00

Cynips quercus-calycis Burgsdorf

The knoppern or acorn gall, also called the Piedmontese gall, and gall of Hungary, which is produced on *Quercus ægilops*, *Quercus pedunculata* and occasionally on *Quercus pubescens* and *Quercus sessiliflora*, occurs in Austria, Hungary, Slavonia, Bosnia, Serbia, Greece, Asia Minor and less abundantly in Germany, Holland, France and Italy. Among the Cynipid galls it ranks next in importance to the Aleppo gall and has been almost as frequently discussed.

In Austria it has been used chiefly by the tanners, but has also been substituted by dyers for the Aleppo gall. This gall, like the Aleppo, is at its best before maturity and should be collected from August to October.

At its height the Knoppern yields from 45 to 50 per cent. of tannin.

CYNIPS KOLLARI Hartig

The Devonshire gall is produced by *Cynips kollari* on *Quercus avellanæ-formis, Quercus fastigiata, Quercus humilis, Quercus ilex, Quercus lusitanica* and varieties, *Quercus mirbeckii, Quercus mongolica, Quercus pedunculata* and varieties, *Quercus pubescens, Quercus pseudoægilops, Quercus rubra, Quercus sessiliflora, Quercus suber* and *Quercus toza.* It occurs in middle and southern Europe, North Africa, Asia Minor, and was introduced into England from the continent early in the nineteenth century. It attracted much attention because of its rapid spread, but the interest in it seems to have been confined to England, as no important reference to it has been found elsewhere.

Attention was first drawn to this gall in England, when it became so abundant that the extermination of the oak forests seemed threatened by it. At that time, about 1858, many notices concerning it appeared in which fear was expressed that it would do irreparable injury to the oaks. But the damage done by it was of no great moment and when the gall was studied it was found to have some tanning and dyeing properties, and to be useful in making an excellent ink.

Many analyses were made of this gall in which varying amounts of tannin were accredited to it. The following was made in 1869 by Watson Smith:

	Per Cent.
Tannic acid	26.71
Gallic acid	Traces only
Woody fiber	47.88
Moisture	20.61
Coloring and loss	4.80
	100.00

RHODITES ROSÆ Linnæus

The Bedeguar of the rose, the gall produced by *Rhodites rosæ* Linnæus, occurs throughout Europe and in western

Asia on eighteen species of *Rosa,* and in North America on *Rosa canina* only. It was highly esteemed by the ancients, but has received very little mention in more modern times as being of any particular use to man.

This gall was mentioned by Pliny as being among the most successful applications for the restoration of hair. For this purpose it had to be powdered and mixed with honey. In Italy it has been used, when powdered and laid on the affected parts, to cure the bite of venomous creatures. This use by the Italians may have grown out of the story related by Pliny that the mother of one of the prætorian guard had a dream, after her son had been bitten by a mad dog, in which she was directed to procure the little round balls at the root of the wild rose and apply them to the affected part. Cuvier has recorded the Bedeguar of the rose as among the remedies successfully used against diarrhœa, dysentery, and cases of stones, scurvy and worms, and as late as 1868 the farmers near Harrogate were known to gather the mossy galls of the rose to make an infusion for diarrhœa in cows, for which they claimed to find it very successful.

Aulax sp. Rübsaamen

The gall of the sage or "Pomme de sauge" is produced by *Aulax* sp. Rübsaamen on *Salvia pomifera* and other species of *Salvia* in the Isle of Crete.

The earliest available record of the use of these galls is that by Belon in 1558 in which he described them as being large as galls, covered with hair and sweet and pleasant to the taste. They were collected at the beginning of May and sold by the people of Candie to neighboring villagers. Olivier stated that "they are esteemed in the Levant for their aromatic and acid flavor, especially when prepared with honey and sugar, and form a considerable article of commerce from Scio to Constantinople, where they are regularly exposed in the market."

Fockeu in 1897 mentions having found these galls in the East but states that to-day the old common name, Baisonge, is unknown and that the people of the country when questioned concerning them said that they had never noticed their existence and expressed doubt of their ever having been used for food, or in making confections.

This name "Baisonge" was not used by either Belon or Olivier for the gall of the sage, but has been used by Cuvier to designate a terebinthe gall from Syria.

Aulax glechomæ Linnæus

Another Cynipid gall which has been used as food is the gall of the ground ivy made by *Aulax glechomæ* on *Glechoma hederacea* L. It occurs in Lorraine and Sweden.

This gall was used in France as food and is said to have an agreeable taste and the sweet odor of the host-plant.

Chinese Oak Gall

An unidentified oak gall, said to closely resemble the European gall, is one which was recorded in Pen T'Sau as Woo-shih-tsze.

The following translation of the note concerning it has been published by Pereira (*Pharm. Journ.*, Vol. 3, 1844, pp. 384–7):

> Woo-shih-tsze also comes from the West, and from India. The tree is said to be sixty or seventy cubits high and eight or nine cubits in circumference, and grows in sandy and stony places. It is compared . . . to the camphire tree. It flowers in the third moon; the flower is white, and rather red in the center. The bud formed is round like a ball; at first green—when ripe, yellowish. An insect eats into it and forms a hole in it. They say that the tree one year produces the Woo-shih-tsze, and another year produces something which resembles a chestnut.
>
> Another name is Whi-ztsip-tsze. It has various medicinal properties. It is used with some other ingredients for dyeing beards black.
>
> The taste of the Woo-pei-tsze is, according to them, a sour, saltish taste—of the Woo-shih-tsze, a bitter taste.

In the Materia Medica of China (Smith, 1871, p. 100) it is called "food for the foodless" and is recommended for medicinal use. It is said to differ little from those of the European market and to have been used formerly in making ink and in dyeing hair.

As this gall is described by the Chinese as coming from the "West" could it possibly be the Aleppo gall, the distribution of which is eastern Europe and western Asia?

Schlechtendalia chinensis (Bell)

Besides the Cynipid galls many others have been recorded as of use to man. Most of them are merely included in the native Materia Medica of China and India, but a few have had other uses.

The most important of these galls is the Chinese gall or Woo-pei-tsze, produced by *Schlechtendalia chinensis* on *Rhus semialata,* in northern India, China and Japan. It has been known and used by the Chinese for many centuries, perhaps even longer than the Aleppo gall has been known in the West. It rivals the Aleppo gall in importance and like the latter is still an important article of commerce.

The Chinese gall has been used in medicine, tanning, and dyeing, and is now imported into Germany and the United States for the manufacture of tannic acid, of which it yields about 70 per cent. As this gall has been fully treated in a paper by A. C. Baker, which has been submitted for publication it is unnecessary to give details here.

Chermes sp. (Baker)

The gall identified by Kirby and Spence as that of *Aphis pini* has been identified by Mr. A. C. Baker as *Chermes* sp., possibly *Chermes lapponicus* Chol, possibly some other. It occurs on spruce-fir in Lapland.

Linnæus states that this gall was used as food, and

Kirby and Spence suggested it as a possible dyeing material. Linnæus's description of it is as follows:

> The extremities of the branches of the spruce-fir bear small yellow cones. . . . When arrived at maturity they burst asunder and discharge an orange-colored powder which stains the clothes of those who approach the tree. I conceive these excrescences to be caused by some minute insects. The common people eat them raw as a dainty, like berries.

It was probably the reference to the orange-colored powder staining the clothes which led Kirby and Spence to suggest that this gall might be placed among dyeing materials.

Pemphigus cornicularis

The gall of *Pemphigus cornicularis,* called in India, Kakra-Singhee, in Syria, Baizonge, and in Europe, gall of the terebinth, occurs in southern Europe and Turkey, in Spain, Syria, China and India.

In India this gall is used in medicine by the natives who assign to it great astringent and tonic properties.

The Hindus have also used it, to a limited extent, in dyeing.

In Thrace and Macedonia Belon recorded it as being collected at the end of June, while still immature, and sold at high prices to the inhabitants of Bource, who used it in coloring fine silks. In Spain, Syria and China it was used as an ingredient in making scarlet dye.

Aldacay Galls

Galls called Aldacay or Caducay galls were recorded by Roxburgh in 1805 as occurring on the leaves of *Mimosa arabica* on the coast of Coromandel. Kirby and Spence in speaking of this gall called the host-plant *Terminalia citrina.*

These galls were said to have been among the most valued of the native dyeing materials and to have been sold in every market. The natives dyed their best and

most durable yellow with them, and they were also used by the chintz painters for their yellows. When mixed with ferruginous mud a strong black dye was obtained.

The astringent properties of these galls were evidently stronger than those of the fruit of the tree, as an ink made from the galls resisted the weather longer than that made from the fruit.

Roxburgh did not identify these galls, but suggested that they might be the "Faba bengalensis" of the old Materia Medica writers. The "Faba bengalensis" according to Bosc is the fruit of the *Myrobolan citrin* altered in its form by the puncture of an insect, but no dyeing properties are ascribed to it. As no further reference to these galls has been found they are still undetermined.

Summary

The important uses of galls have been in medicine, the manufacture of ink, tanning and dyeing, with a few references to their use as food, and one to their use as fuel.

In medicine the following galls have been used: *Andricus fœcundatrix* Hartig, *Cynips* sp. Cuvier on field cirsium, *Cynips gallæ-tinctoriæ* Olivier, *Cynips polycera* Giraud, *Cynips quercus-folii* Linnæus (*Cynips quercus-terminalis*) = *Biorhiza pallida* Olivier, *Cynips quercus-tozæ* Bosc, *Pemphigus cornicularis, Pemphigus pallidus, Rhodites rosæ* Linnæus, *Schlechtendalia chinensis* (Bell) and the undetermined ones: Chinese oak gall, Istrian gall, Marmora gall, galle corniculée, and Bazgendge (Fockeu) or Chersamel on *Tamarix*.

In the manufacture of ink the galls used are: *Cynips gallæ-tinctoriæ* Olivier, *Cynips kollari* Hartig, *Schlechtendalia chinensis* (Bell), the Aldacay or Caducay galls, the Istrian, Marmora, Morea and Smyrna galls and others from France, Italy, Hungary, Senegal and Barbary.

For tanning the following have been found useful: *Cynips gallæ-tinctoriæ* Olivier, *Cynips hungarica* Hartig, *Cynips insana* Westwood, *Cynips kollari* Hartig, *Cynips*

lignicola Hartig, *Cynips quercus-calycis* Burgsdorf and *Schlechtendalia chinensis* (Bell).

For use in dyeing have been recorded: *Cynips gallæ-tinctoriæ* Olivier (*Cynips tinctoria-nostra*) = *Cynips infectoria* Hartig, *Cynips insana* Westwood, *Cynips kollari* Hartig, *Cynips quercus-calycis* Burgsdorf, *Cynips quercus-petioli* Linnæus, *Pemphigus cornicularis*, *Schlechtendalia chinensis*, possibly *Chermes* sp. Baker, and the undetermined galls, Aldacay or Caducay galls, the gall-nut used by the Somali women for a tattooing dye, Baizonge Cuvier and Bazdyendge Pomet.

As food, only a few galls have been used: *Aulax* sp. Rübsaamen or Baisonge Fockeu, *Aulax glechomæ*, *Cynips* spp. Girault, *Disholcaspis weldi* (Beutenmüller), *Callirhytis* sp.? Hopkins, *Chermes* sp. Baker and *Schlechtendalia chinensis*. In the case of the last named the gall itself is not eaten but the powder found on the outside is used for seasoning soup.

As fuel for lamps the Greeks used *Cynips theophrastea* and an undetermined gall called by Pliny the black-gall-nut.

Common Names of Insect Galls

In the following list of the common names of the insect galls which have been of any practical use, will be found a number of names for the gall of *Cynips gallæ-tinctoriæ* and several for that of *Schlechtendalia chinensis*. To avoid confusion I would suggest that for the former the name Aleppo gall be adopted, and for the latter the name Chinese gall, as it is under these names that they are designated in the commerce reports, in some of the trade journals and in the technical works on dyeing, tanning and ink manufacture.

Acorn gall .... *Cynips quercus-calycis* Burgsdorf
Aleppo gall .... *Cynips gallæ-tinctoriæ* Olivier
Baisonge Fockeu .... *Aulax* sp. Rübsaamen
Baizonge Cuvier .... *Pemphigus cornicularis*
Bara Mai .... Hindu name of a gall on *Tamarix gallica*

Bazdyendge Pomet ....Turkish name for a gall on oak
Bazgendge Fockeu ....Turkish name for a gall on *Tamarix orientalis*
Bedequar of the rose ....*Rhodites rosæ* Linnæus
Black gall-nut Pliny ....Undeterminable
Black oak wheat ....*Callirhytis* sp.? Hopkins
Bussorah gall ....*Cynips insana* Westwood
Chersamel ....Egyptian name for Bazgendge (q.v.)
Chinese gall ....*Schlechtendalia chinensis* Bell
Chinese pear gall ....*Schlechtendalia chinensis* Bell
Chota Mai ....Hindu name for a gall on *Tamarix orientalis.*
Dead Sea fruit ....*Cynips insana* Westwood
Devonshire gall ....*Cynips kollari* Hartig
Fruits for the foodless ....A Chinese oak gall
Faba bengalensis ....A gall on *Terminalia chebula*
Gall of commerce ....*Cynips gallæ-tinctoriæ* Olivier
Gall of field cirsium ....*Cynips* sp. Cuvier
Gall of sage ....*Aulax* sp. Rübsaamen
Gall of *Mimosa arabica* Roxburgh . ?*Faba bengalensis*
Gall-apple ....*Cynips gallæ-tinctoriæ* Olivier
Gall-nut Burton ....Undeterminable
Galle de France ....*Cynips kollari* Hartig
Galle en artichaut ....*Andricus fœcundatrix* Hartig
Galle corniculée Guibort ....Undeterminable
Gul-i-pista ....*Pemphigus pallidus*
Hungary gall ....*Cynips quercus-calycis* Burgsdorf
Ink marble ....*Cynips gallæ-tinctoriæ* Olivier
Istrian gall ....Undeterminable
Japanese gall ....*Schlechtendalia chinensis* Bell
Kakra Singhee ....*Pemphigus cornicularis*
Knoppern ....*Cynips quercus-calycis* Burgsdorf
Levant gall ....*Cynips gallæ-tinctoriæ* Olivier
Mad apple of Sodom ....*Cynips insana* Westwood
Marmora gall ....Undeterminable
Mecca gall ....*Cynips insana* Westwood
Nut-gall ....*Cynips gallæ-tinctoriæ* Olivier
Nut-gall ....*Schlechtendalia chinensis* Bell
Oak apple ....*Andricus quercus-californicus*
Oak-apple galls ....*Cynips* spp. Girault
Oriental gall ....*Cynips gallæ-tinctoriæ* Olivier
Piedmontese gall ....*Cynips quercus-calycis* Burgsdorf
Pomme de chene Guibort ....Undeterminable
Small crown gall of Aleppo ......*Cynips polycera* Giraud
Sumrat-úl-asl ....Arabic name for *Chota Mai* (q.v.)
Sumrat-úl-túrfa ....Arabic name for *Bara Mai* (q.v.)
Turkey gall ....*Cynips gallæ-tinctoriæ* Olivier
Wheat mass [Mast] ....*Callirhytis* sp.? Hopkins
Whip-ztsip-tze and Woo-shih-tsze . . A Chinese gall on oak
Wu-pei-tsze ....*Schlechtendalia chinensis* (Bell)

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CONTINUOUS AND DISCONTINUOUS VARIATIONS AND THEIR INHERITANCE IN PEROMYSCUS

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I. Introduction

Many of the views which we are now accustomed to associate with the names of Weismann, Bateson, DeVries, Nilsson-Ehle and others were either foreshadowed or clearly formulated by Francis Galton, many years earlier. Galton's polygon, by which he illustrated the difference between continuous and discontinuous variations, is doubtless known to most readers; as is also his distinction between "blended" and "particulate" inheritance. It is less familiar, perhaps, that Galton regarded all inheritance as "largely, if not wholly, 'particulate.'" Even skin color, the classic example of blended inheritance in man, is presumably "none the less 'particulate' in its origin, but the result may be regarded as a fine mosaic too minute for its elements to be distinguished in a general view." Again, "the blending in stature is due to its being the aggregate of the quasi-independent inheritances of many separate parts" (1889, p. 139).

Galton did not deny all heritability to those variations which were represented by the minor oscillations of his polygon, although he refers to such variations as "unstable."

With the modern revival of Mendel's principles of

heredity and the definite formulation of a "mutation theory" of evolution, some of Galton's more or less tentative views have crystallized into dogmas. Along with the two just mentioned, there has been incorporated the principle of the "continuity of the germ-plasm," a conception which was likewise first clearly formulated by the great English geneticist, though its modern expression we owe to Weismann.

These various hypotheses have been woven together into a single fabric and made to reinforce one another. It will hardly be denied that some rather flimsy reasoning has been employed at times by those here concerned. Thus one familiar syllogism runs somewhat as follows: Somatic modifications are not inherited; fluctuating variations are not inherited; therefore fluctuating variations are somatic modifications. Indeed, "somatic" and "non-hereditary" have come to be used interchangeably by many writers. Whether or not somatic modifications ever become germinal is a matter to be settled by evidence. But I must confess that I have never regarded as self-evident the contention that because characters are found to be "non-hereditary" they are, *ipso facto*, "somatic" in origin.

A certain sanctity and inviolability has come to be attached to the units of heredity or "genes," according to the neo-Mendelian creed. Not only do these units refrain from any degree of blending, but—save for occasional mysterious "mutations"—they are quantitatively and qualitatively unchangeable. Thus, the only differences upon which selection, natural or artificial, can act are differences due to the presence or absence of different genetic factors. "We know," say the Hagedoorns, in an article (1917) which is typical of much of the recent literature of heredity, "that all the different genes, all the different inherited factors . . . are each in themselves invariable. . . . Liability to change by selection is synonymous with genotypic variability, and this true variability is synonymous with impurity."

Much dialectic skill has been displayed in maintaining this set of opinions against the many facts which seem directly to refute them. Indeed, it must be conceded that a fairly consistent and logical edifice has been erected upon these foundations. Strictly logical, though oftentimes improbable interpretations have been given to each new volley of hostile data, until the fortress has begun to seem impregnable—at least to a frontal attack.

But perhaps, of late, another metaphor has come to suit the situation better—that of the two knights fighting on opposite sides of the same shield. The Mendelians have recently had recourse to more and more minute factorial differences in explaining certain lesser gradations of color in some of their material, until at length the distinction between their opponent's "continuity" and their own "discontinuity" is more imaginary than real. Water is a continuous medium for all the ordinary purposes of life, and solutions of different substances may be completely "blended" therein. Its resolution into hypothetical molecules, atoms, electrons and the like does not in the least affect these fundamental facts.

The publication of the data which I offer in the present paper confessedly does not constitute a "frontal attack" upon the multiple factor hypothesis. My results belong to a class of facts which have already figured extensively in this controversy, and which have been met by ingenious and plausible counter-arguments. As I have stated elsewhere, I am led to doubt very seriously whether any *conceivable* evidence could be brought forward which would be admitted by the more extreme neo-Mendelians to be really damaging to their position. As in so many other cases, the victory is to be won, if at all, through a process of "attrition." Positions are gradually abandoned which are never *disproved* in a logical sense. Indeed, as hinted, above, there are clear signs that the defenders of the "multiple factor" explanation of selection and blended inheritance are already retiring from their main positions.

II. The Distribution of Subspecies

The term *subspecies,* as here employed, is nearly equivalent to *geographic race.* These subdivisions of a species occupy different, though often contiguous areas. When contiguous, they are said to intergrade completely with one another along the boundaries of their respective territories; and in any case, their ranges of variation overlap broadly. It is this fact, indeed, which leads to their being ranked as subspecies, rather than as distinct species, since the differences between some of the more widely separated among them would be quite sufficient to give them specific rank were there no connecting forms.

In such reports as those of Osgood on *Peromyscus* (1909), Nelson on the rabbits (1909), or Goldman on *Neotoma* (1910), the geographic ranges of certain species are seen to be divided up into what look like quite arbitrary subdivisions, corresponding to the ranges of the component subspecies. The boundaries between these subdivisions oftentimes follow certain natural barriers, but in some instances this does not appear to be true. And, in any case, it is doubtful whether any geographic barrier, save a continuous body of water or a lofty and unbroken range of mountains could prevent the free diffusion of such rodents. These minor areas, furthermore, frequently comprise territory having a very wide diversity of physical conditions. For example, *Peromyscus maniculatus gambeli* is represented as ranging from the foggy coastal area of central and southern California across the hot, semiarid San Joaquin Valley to the snowy heights of the Sierra Nevada. And in latitude, its range is said to extend roughly from the 31st to the 48th parallel.

According to Osgood,

> Specimens from Monterey, the type locality, are absolutely identical with those from San Diego and the northeast coast of Lower California, and the intervening region is inhabited by exactly the same form. These, moreover, are like specimens from . . . the west slope of the Sierra (p. 69).

We might well be puzzled to discover any common ele-

ments of the physical environment which were responsible for the presence of the same subspecies under such widely divergent conditions of life. Particularly is this true when the environmental differences, as in the present case, far exceed those between the habitats of certain quite distinct subspecies.

Nor does the contention seem justified that such extensity in the distribution of a single subspecies is fully accounted for by the absence of any insurmountable barriers to its dispersal. So far as geographic features are concerned, the barriers between the range of *gambeli* and the ranges of certain neighboring subspecies seem to be no greater than some of those which traverse the territory of *gambeli* itself. Looking at the distribution maps in such publications as those just mentioned, one is impressed by a seeming analogy between the boundaries of these various subspecific ranges and those of the political subdivisions of the earth's surface. In considerable degree these last are bounded by geographic features, but to a large extent, also, the lines of demarcation seem to be drawn quite arbitrarily—the territories merely bound one another.

While great weight must be given to the findings of these taxonomic experts, I think it is our duty at present to accept certain of their conclusions with considerable reservation. This is particularly true of assertions as to the *absolute identity* of the characters of specimens from widely different parts of a given range. The published data make it plain that the authors are in no position to detect minor differences of a statistical nature. A small number of specimens from each locality are commonly compared, the measurements "in the flesh" of the various specimens necessarily having been made by a number of different collectors. It will be evident from the ensuing pages that the differences with which we are dealing are often of such a nature as to be revealed only by the comparison of large numbers of individuals, measured according to uniform standards. As regards the

latter point, tests which I have made of the standards of measurement employed by several competent collectors show clearly that the differences due to "personal equation" are sometimes at least as great as those which characterize quite distinct local races.

Accordingly, we might feel justified *a priori* in entertaining some skepticism as to the homogeneity of these races of animals throughout such great areas. Furthermore, I already have a certain amount of direct evidence which renders this contention improbable. Such evidence will be considered later.

An extremely desirable undertaking would be to run a series of trapping stations through the territories of two

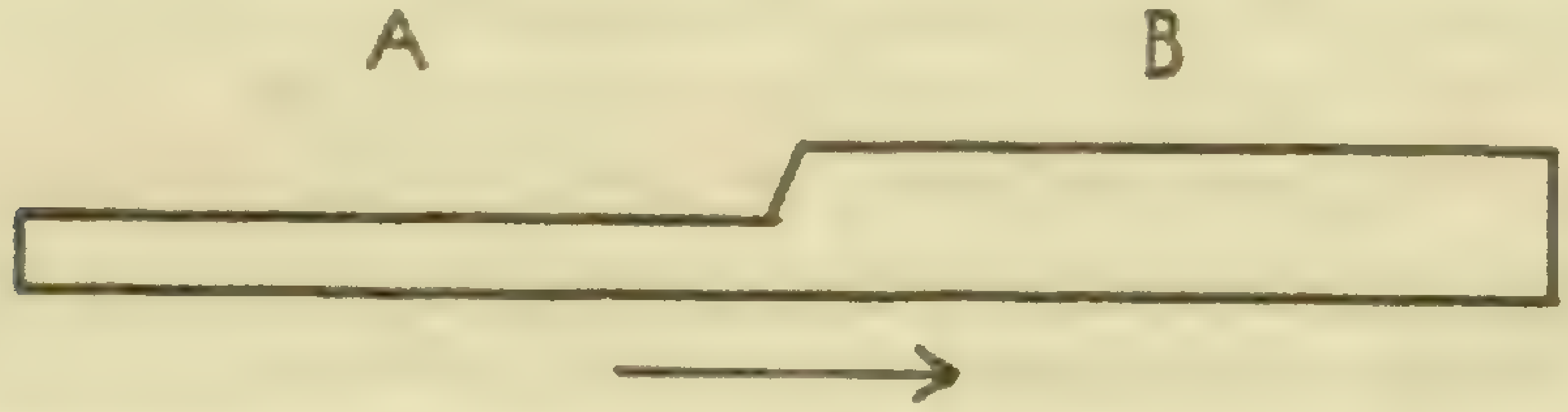

FIG. 1.

adjacent subspecies, at right angles to the supposed line of demarcation. This the author hopes to do in the course of time, though the task is not as simple as might perhaps be anticipated. Theoretically, a number of possible conditions might be revealed by such an investigation.

In the first place, it might be found (Fig. 1) that each of the two races was, in reality, "absolutely identical"

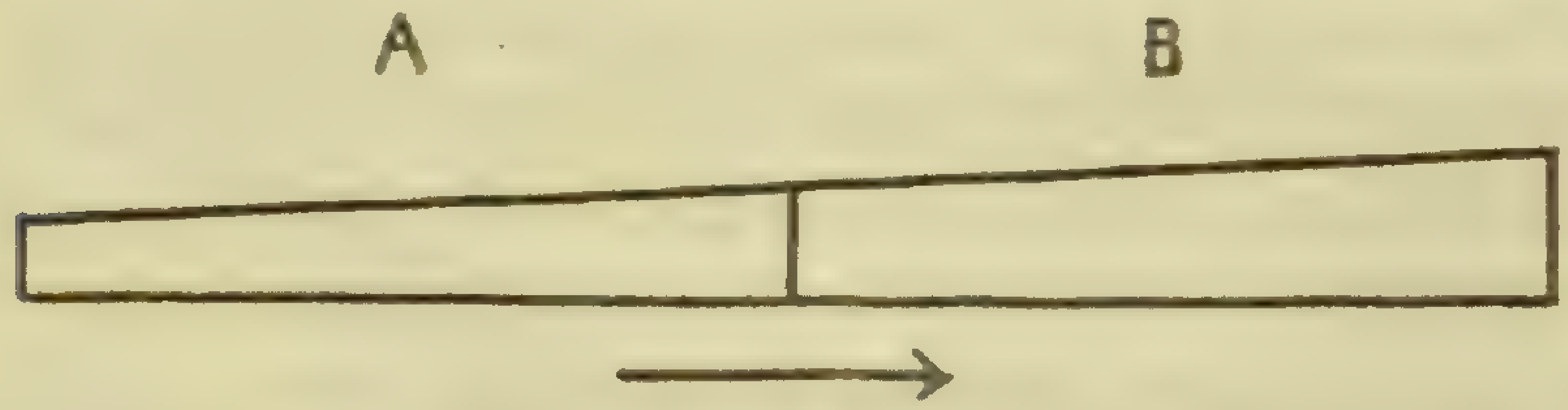

FIG. 2.

throughout its own range, while the transition between the two might be fairly abrupt.

Secondly, there might be an unbroken intergradation, in respect to the differential characters, throughout the

entire ranges of both the races (Fig. 2). In this case there would be no real boundary between the two groups, and indeed the recognition of two subspecies, rather than one or three, would be quite an arbitrary procedure.

Finally, there might be a condition, less easy to represent by diagrams, in which neither race was completely homogeneous, each being subject to considerable local variation within its own territory. Such local differences might or might not tend to be graduated as indicated in Fig. 2. Or, there might be some degree of gradation with respect to certain characters (*e. g.*, pigmentation), but not with respect to others (*e. g.*, length of appendages). In such circumstances, the recognition of two "subspecies" would depend upon the fact that the population of each of the respective territories was *relatively* uniform, and the changes encountered at the boundary *relatively* abrupt.

I am not yet in a position to say with certainty which of these possibilities is realized in the case of the species with which I am dealing (*Peromyscus maniculatus*), but I already have some strong evidence that the third one most nearly represents the actual state of arairs. As regards depth of pigmentation, we certainly find something approaching a graded series as we pass from the interior desert regions of California toward the coast, or as we pass from the coast of southern California, northward into successively more humid regions, as far as Alaska. But here we are dealing with a number of "subspecies." I have grounds for believing, however, that similar gradations occur within areas conventionally assigned to single subspecies.

Other questions of high theoretic importance relate to the nature of the animals inhabiting the so-called "areas of intergradation." Does this intermediate population manifest a complete blending of all the subspecific characters, or does it consist of a mixture of individuals, severally exhibiting the respective racial characters in a fairly pure state, or may there be a mosaic condition more

directly suggestive of Mendelian segregation? A definite answer to these questions I am likewise obliged to defer for the present.

Truly representative collections have been made by me thus far at only four stations within the State of California, though various other points have been visited and considerable numbers of the mice have been trapped there. My four principal collecting stations are located near Eureka, Berkeley, La Jolla and Victorville.[1] Meteorological records were kept for about two years at each of these points. These records have not thus far been carefully analyzed, however, so that their publication must be postponed. A preliminary comparison of climatic conditions at these four points has already been made (Sumner, 1915*a*). It will suffice, for present purposes, to state that, as regards both atmospheric humidity and rainfall, these stations rank (from highest to lowest) in the order given above, *i. e.*, Eureka, Berkeley, La Jolla and Victorville; while as regards mean annual temperature the reverse order holds.

The distribution of the three subspecies of *Peromyscus maniculatus*, recognized by Osgood as occurring within the limits of California, is represented in Fig. 3. It will be seen that one of my stations (Eureka) lies within the range of *rubidus*, another (Victorville) within the range of *sonoriensis*, while the other two (Berkeley and La Jolla) lie within the range attributed to *gambeli*.

In the ensuing pages, I am not in the least concerned with characterizing and defining those taxonomic groups which have been called *Peromyscus maniculatus gambeli*, *rubidus* and *sonoriensis*. I shall merely discuss the differences between (and within) four representative collections taken by me in widely separated and climatically different regions of the state. The question as to what "subspecies" a given mouse "belongs to" is for my purposes a distinctly minor consideration.

[1] Four other stations have been added since the present paper was written, but the data derived from these can not be included here.

FIG. 3. Distribution of the recognized subspecies of *Peromyscus maniculatus* in California and Nevada, according to Osgood, 1909 (from Sumner, 1915). The heaviest shading denotes the range of *P. m. rubidus*, the intermediate shading that of *gambeli*, the lightest that of *sonoriensis*. Supposed areas of intergradation between two races are indicated by dotted lines.

III. Differences between the Four Local Races under Consideration[2]

These differences may be divided, for the sake of convenience, into pigmental and structural ones. Since the former are the most obvious, they will be discussed first.

1. *Pigmental Differences*

The pigmental differences relate to (1) the hair, (2) the skin.

Hair.—Like the other members of the genus *Peromyscus,* the mice of the present group are covered with pigmented hairs upon the dorsal and lateral surfaces, while the ventral surface and to a large extent the feet are covered with white hair. Upon the trunk these white hairs are, to be sure, devoid of pigment only at the distal ends. Parting the pelage at any point, dorsal, ventral or lateral, reveals the presence of a slate-colored basal zone in each hair.

The most obvious differences between the races under consideration relate to the dorsal coat color (Fig. 4). This is darkest in the animals from the humid redwood district (Eureka), palest in those from the Mojave Desert (Victorville), and of an intermediate hue in the collections from Berkeley and La Jolla. These last two races likewise differ from one another, the former being darker than the latter. Thus we have a series of four gradations, which are correlated directly with gradations in the rainfall and atmospheric humidity of their respective habitats.

It is important to notice, however, that these differences of shade relate rather to averages than to individual cases. *All* of the Eureka mice are not darker than *all* of the Berkeley mice. Nor are all of the Berkeley mice darker than all of the La Jolla mice, nor all of the latter darker than all of those from Victorville. In comparing repre-

[2] I here use the word "race" as being a non-committal term, elastic enough to cover any two collections of individuals which show significant differences of type.

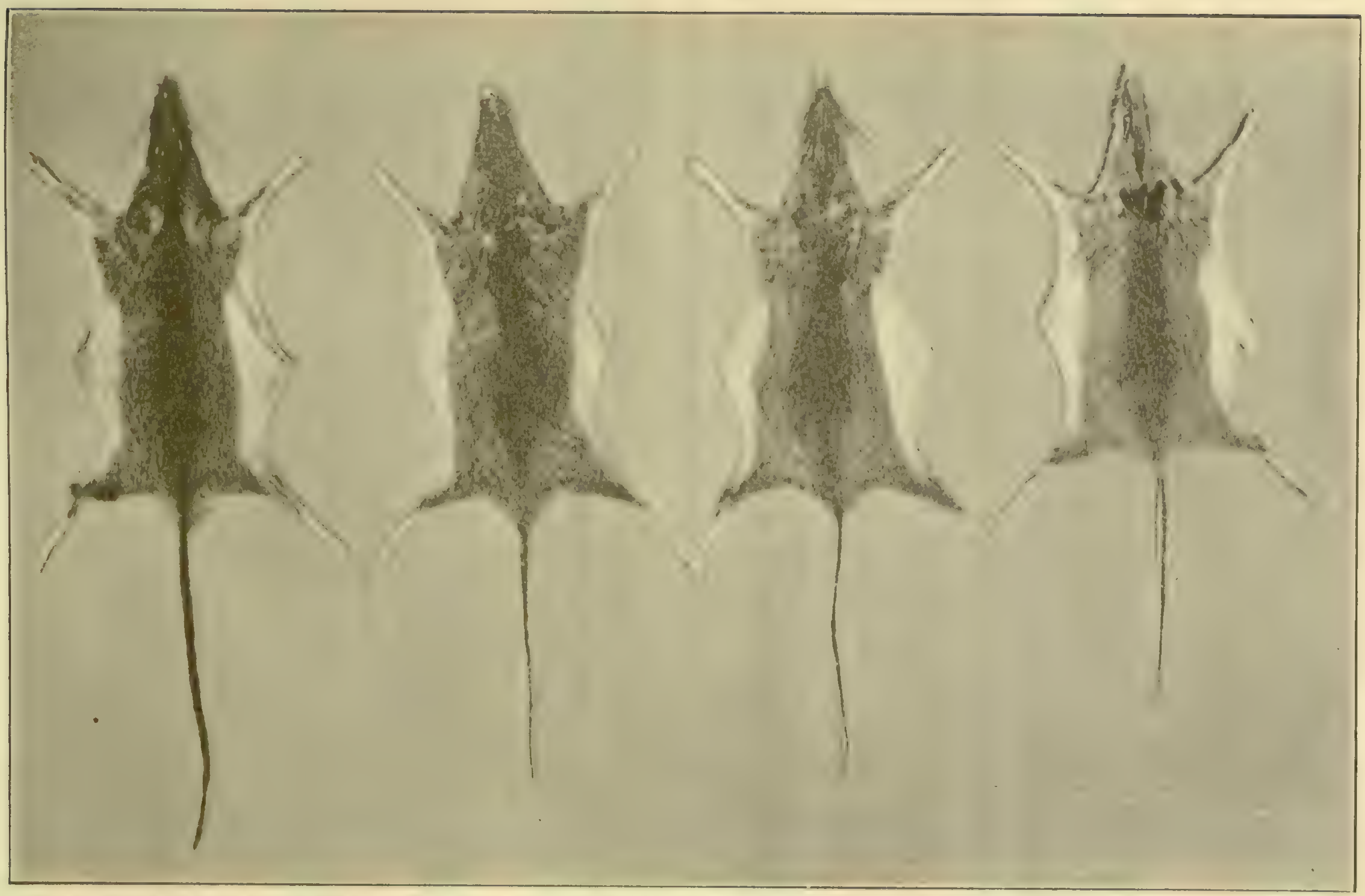

FIG. 4. Skins of male adult wild specimens of the Eureka, Berkeley, La Jolla and Victorville races of *Peromyscus maniculatus*, in order named. The skins have been selected with a view to showing the average shade of each series.

sentative collections of any two adjacent races belonging to this series, there is found to be a broad zone of overlapping. That is to say, there are many individuals in each set which, so far as color goes, could be equally well placed in either. I have, for example, laid out in parallel rows considerable numbers of *sonoriensis* and the La Jolla form of *gambeli,* and found that the darker half of the former set completely overlapped the paler half of the latter. While no confusion would be possible between the paler *sonoriensis* and the darker *gambeli,* there were a large number of specimens which could only arbitrarily be assigned to either "subspecies." Indeed, it is freely admitted by systematists that in many cases they can assign a given specimen to its proper subspecies only if they know the locality at which it was trapped. No such confusion would be possible, however, between the more divergent races of our series, *e. g.,* those from Eureka and the desert. I have never seen a *rubidus* which could not, by color alone, be readily distinguished from *sonoriensis* and vice versa.

Any attempt to give verbal equivalents for these color differences is highly unsatisfactory. In a later report I expect to undertake the analysis of these shades by means of a color wheel. For the present I will content myself with a very brief statement.[3] The dorsal darker stripe of the Eureka mice is of a shade lying somewhere between Ridgway's "sepia" and black, the paler lateral region lying between "Saccardo's umber" and "sepia."[4]

[3] The ensuing remarks apply only to the mature pelage. These mice pass through three distinct pelage phases: (1) the juvenal, which, in all races, is neutral gray in hue, and considerably darker than the adult shade; (2) the post-juvenal or adolescent, commonly paler and yellower than the last; (3) the mature or adult pelage, which is still more highly colored and frequently of still paler shade. The first molt occurs some time during the second month after birth, the second some time between the age of six months and a year. The various races of mice here considered, and even the mutants, are probably as clearly distinguishable in the immature pelages as they are in the adult.

[4] See Ridgway, 1912. "Dresden brown" and "mummy brown" perhaps approximate the shades in question as well as the last two mentioned.

Since the coat color is at no point homogeneous, any such comparison with uniformly tinted paper is of course very crude.

The desert mice are of a hue which can not even approximately be represented by reference to Ridgway's "color standards." The effect is probably not far from that which would result from a mixture of fine streaks of black and of "ochraceous buff" or "cinnamon buff," so proportioned as to approximate the general hue of the barren soil. As in all of these races, the mid-dorsal pelage is commonly darker than the lateral. All that need be said of the two collections of "*gambeli*" is that they are intermediate between the extreme types just referred to.

As a special case of the general hair color of the body, though not entirely correlated with this, is to be mentioned the color of the "ankle" region. The latter, particularly on its ectal surface, is covered with very short pigmented hairs, whose depth of shade affords another feature distinguishing the average condition of these four races.

I have given considerable attention to a microscopical examination of the hairs of these various mice. In position the pigment is of two different sorts, axial and superficial, located in the medulla and cortex respectively. A series of more or less disc-shaped, black pigment bodies extend from the base of each hair throughout the whole, or a considerable part, of its length. In the stouter hairs, there are, in the expanded region, two to four longitudinal rows of these bodies. In all cases, they alternate regularly with air spaces.

In the all-black hairs, the black pigment extends very nearly to the extreme tip. In the banded hairs, a region of varying length occurs in the distal half, in which the black pigment gives place to yellow. The dark pigment does not end abruptly, however. The dense black bodies become fragmented into their component rounded granules, as we pass from one segment to another, first giving

way to scattered collections of these granules (which are dark brown when seen singly) and later disappearing altogether. In the transitional region, black and yellow pigment may frequently be found in the same segment. In most hairs, the dark bodies again replace the yellow ones as we pass toward the tip; occasionally the yellow continues as far as any axial region is distinguishable.

The yellow pigment seems to be restricted to the axial part of the hair. To some extent, it occurs in the form of granules, but, unlike the black, it is largely present in a diffuse condition. This pigment is not all of the same tint, but varies in shade from a pale yellow to an orange or even a very pale brown.

For a varying length, on the distal, tapering ends of nearly all the hairs of the colored parts of the body, there is a very dark, granular pigment, lying close beneath the surface of the hair. This overlies and reinforces the axial pigment, so that the distal end is frequently darker than any other part of the hair. The superficial pigment, where dense, commonly looks almost black, but when seen in a thin layer the single granules appear brown. As already stated, this is likewise true, though in lesser degree, of the "black" axial pigment. In one of the "mutants," to be described later, this distal dark zone is nearly or quite lacking, and the same is true of certain exceptional samples of hair taken from normal individuals.

The yellow pigment is readily soluble in even fairly dilute potassium hydrate solutions, whereas the dark pigment is very much more resistant to this reagent, and may remain unchanged, even after the complete disintegration of the hair.[5]

Most students of this subject seem to follow Miss Durham (Bateson, 1903) in recognizing three pigments in the hair of *Mus musculus*—the black, the brown or chocolate, and the yellow. After considerable examination of the

[5] I have, however, observed preparations in which even the densest black pigment bodies assumed a reddish brown color, especially near the margin of the cover-glass.

hair both of *Mus* and *Peromyscus*, I can not feel sure of any sharp distinction between the black and the brown pigments. It is true that the axial pigment bodies of the basal portions of the hair are nearly dead black, while most of the superficial pigment at the distal ends is distinctly brown. But all gradations occur in the axial pigment of the transitional zones, and these gradations appear to be due not merely to differences in the density of the clusters of granules, but to gradations in the depth of color of the individual granules themselves. Without having made any careful chemical tests, I am disposed to believe that black and brown, in the hair of mice, are due merely to different degrees of aggregation of a single pigment. On the other hand, this dark pigment seems to differ, chemically and otherwise, from the various shades of yellow.

The differences in the color of mice of different subspecies and of different parts of the pelage of a single individual appear to be due to two chief causes: (1) the relative length of the pale zone, in relation to the rest of the hair; and (2) the proportionate numbers of the all-dark and of the banded hairs; probably also to (3) the depth of shade of the yellow pigment in the pale zones, and (4) the degree of concentration of the superficial pigment at the distal ends. In some of the "mutants," as will be pointed out below, certain other factors contribute to the differences shown.

Of importance for our general viewpoint is the fact that no one of the geographic races which has been examined possesses any type of hair which is wholly lacking in any other race. It would be impossible from a single hair, or even a small group of hairs, to say from what sort of mouse they were taken.

When viewed on the ventral side, these four races of mice likewise present characteristic differences. They form a graded series in respect to the whiteness of the pelage, which is purest in the desert race and least so in that from the redwoods. The differences are found to

result from the relative length of the terminal pigmentless zone which is present in these hairs. The ventral hair of the desert race also appears to be somewhat longer, or at least of a softer texture, than that of the others.

In the case of the ventral surface, like that of the dorsal, these differences relate to averages rather than to individuals. Likewise, it is of interest to note that within each race there is little or no correlation between the dorsal and the ventral shade. I have frequently graded a considerable row of mice of a single race in respect to the shade of the dorsal pelage, and found, on turning the animals over upon their backs,[6] that the order of arrangement did not correspond with the ventral gradations of shade.

Another differential character of these races is the degree of lateral extension of the ventral white area of the body, or, conversely stated, the ventral extension of the dorso-lateral pigmented area. The colored and uncolored regions of the body come together abruptly along an irregular lateral line extending from the snout to the tip of the tail. In the desert race, more of the white ventral region is usually to be seen in side view than is seen in the darker races. The gradation of the other three races among themselves is less obvious.

This degree of extension of the colored area relates not merely to the body but to the appendages. In the darker races an elongated tongue commonly extends down upon the fore-limb, in some cases even to the hand, while in *sonoriensis* such a ventral projection is usually little developed. The graduation of our four races in regard to this character corresponds to that noted in respect to shade. Similar conditions are observable on the hind limbs, particularly upon the ankle, where the pigmented hair may extend as far as the heel, or may fall short of this in varying degrees. The case of the tail will be discussed separately.

A hair character which seems to be peculiar to *sonoriensis,* among the races here considered, is the presence of

[6] Fresh specimens, not skins, are used for most of these comparisons.

small clusters of white-tipped hairs near the anterior insertions of the ears. But even this feature is not evident in all individuals.[6a]

Many species of *Peromyscus,* including the *maniculatus* series, have what is known as a "bicolored" tail. The hairs throughout a longitudinal stripe of varying width, upon the dorsal surface of this member are dark brown or black, while those of the ventral side are white. Now a casual inspection serves to show that this caudal stripe is broader and darker in the Eureka mice than in the desert ones, while a more careful comparison shows that the "*gambeli*" individuals are, on the whole, intermediate between the other two.

Fortunately, the breadth of this stripe is a character which may be subjected to fairly accurate measurement. It is my practice to slit the skin of the tail along the mid-ventral line, strip it off, and press the inner, damp surface firmly against a strip of black cardboard. The total width of this skin (= circumference of tail) is then taken at the mid-point of its length; likewise the width of the tail stripe. The ratio between the two readings is next determined, the width of the dorsal stripe being expressed as a percentage of the circumference of the tail. The following are the figures for the four races and the two sexes, the figure in parenthesis representing the number of animals measured:[7]

TABLE I

rubidus, ♂ (69)	42.51 ± 0.45
rubidus, ♀ (50)	41.96 ± 0.53
Berkeley *gambeli,* ♂ (24)	36.08 ± 0.80
Berkeley *gambeli,* ♀ (28)	35.50 ± 0.56
La Jolla *gambeli,* ♂ (85)	32.08 ± 0.33
La Jolla *gambeli,* ♀ (46)	32.43 ± 0.49
sonoriensis, ♂ (74)	27.49 ± 0.32
sonoriensis, ♀ (59)	28.92 ± 0.36

[6a] This condition I have recently found to occur in occasional specimens of *rubidus* trapped near Carlotta, California.

[7] Since this character was not measured when these studies were first commenced, the number of individuals included in the present table falls far short of those measured for some other characters.

While the statistical certainty of these four types can not be doubted, it must again be insisted that the differences relate to averages rather than to individual animals. The frequency distributions of the various widths, as represented by the histograms (Fig. 5), show this point clearly. There is a certain amount of overlapping, even between the most divergent races.

Skin Pigmentation.—Certain regions of the skin are colored by dark pigment. The regions showing skin pigmentation most clearly are the ears, tip of snout, soles of feet, and, in the males, the scrotum.

Frequent comparisons of considerable numbers of freshly killed specimens have made it plain that, in respect to the pigmentation of the ears, our four races can be arranged in the same graded series as was found to hold for coat color. As regards the other three skin characters, I have never compared more than two races at a time, but I feel little doubt that all four could be arranged in the same order. No exact measurements are here possible, as in the case of the tail stripe. In a few instances I have, however, graded a given character, according to an arbitrary scale, and have thus been able to express the differences between two races in a roughly quantitative way. The following comparison between 42 *sonoriensis* and 38 La Jolla *gambeli* with respect to the pigmentation of the scrotum will illustrate this point.

TABLE II

	sonoriensis		*gambeli*	
	Number of Cases	Percentage	Number of Cases	Percentage
Heavy	1	2.4	3	7.9
Moderate	3	7.1	2	5.3
Slight	5	11.9	7	18.4
Very slight	1	2.4	4	10.5
None	32	76.2	22	57.9
Total	42	100.0	38	100.0

A similar tabulation was made in another case, comparing two lots of specimens of these same races in respect to the pigmentation of the foot.

It might readily be contended that all these various pigmental differences, which have thus far been considered, are merely manifestations of some general tendency toward a given degree of pigmentation of the body as a

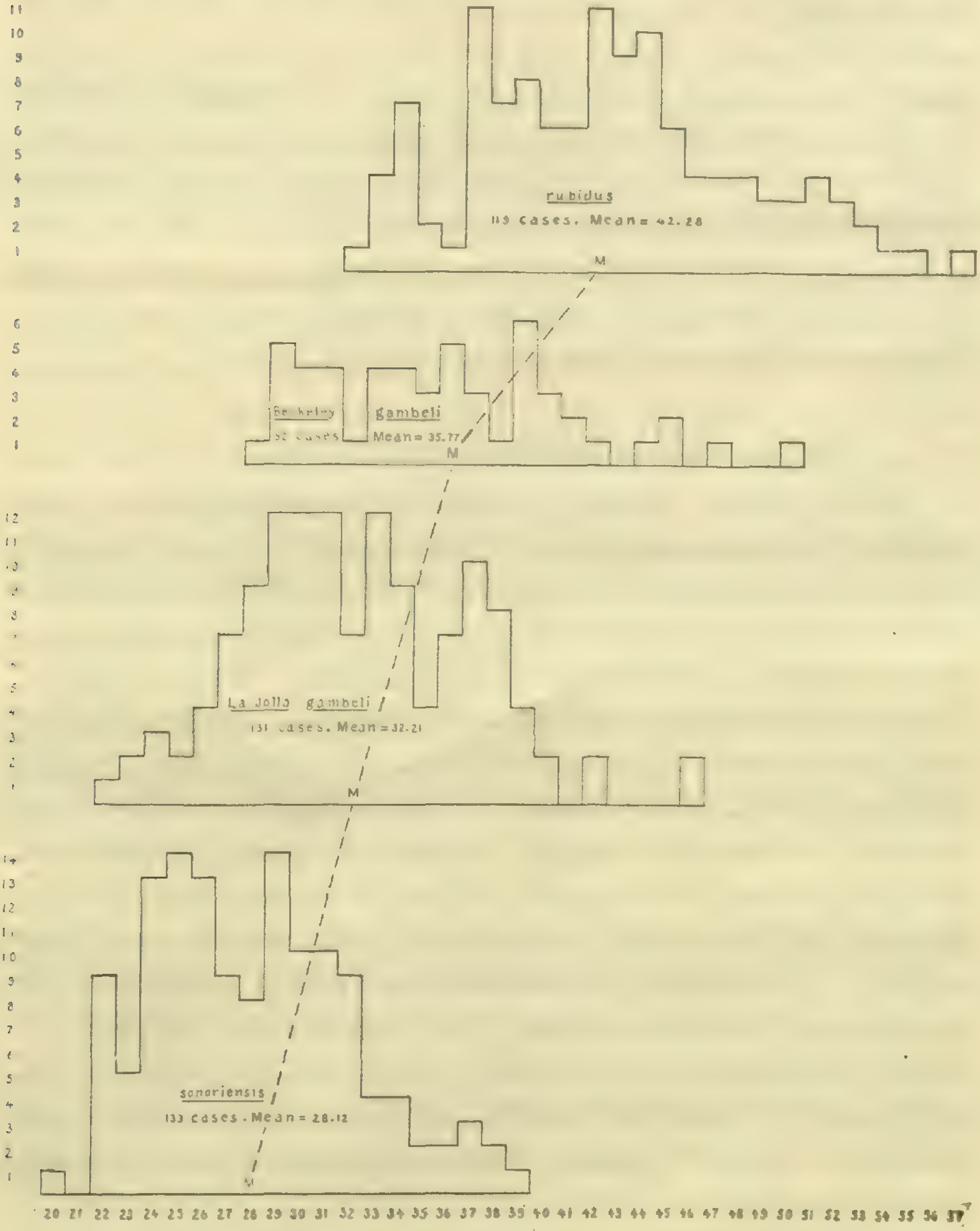

FIG. 5. **Histograms, showing the frequency distributions of the percentage values for the width of the tail stripe (ratio to circumference) in the four races here considered (sexes combined).**

whole. This tendency perhaps manifests itself in a greater or less intensity or extensity, or both. In the absence of exact quantitative standards, it is impossible

to determine whether or not these various pigment characters are correlated. If they are, the correlation is certainly not a close one, as frequent observations have shown. For example, the grade of foot-pigmentation was determined for the paler and darker halves of a series of *sonoriensis* and also for a series of *gambeli*. In both cases the average grade for the foot was slightly greater for the darker half than for the paler; but the difference was so small that I am not sure of its significance. Again, in the lot of 38 *gambeli* comprised in Table II the darkest individual (dorsally) and the one with the darkest feet were both devoid of visible pigment on the scrotum. Similar entries are frequent among my notes.

2. *Structural Differences*

The structural features which I have subjected to quantitative determination are (1) *weight,* (2) *body length,* (3) *tail length,* (4) *foot length,* (5) *ear length,* (6) *number of tail vertebræ;* together with several other skeletal characters which I shall not discuss in the present paper. The methods employed throughout these studies will be described more fully in a later report. A brief statement will suffice for the present. Body length, as here employed, is the total length, minus the length of the tail. In taking the total length, a special contrivance is employed, the body being stretched slightly and to a uniform extent. A constant procedure is likewise employed in measuring the tail length. The figure recorded for the latter represents the distance from the first free caudal vertebra to the tip of the tail, under a uniform degree of tension. The ear length here used is that from the summit of the "notch" to the tip of the ear. Foot length is the distance from the heel to the tip of the claw of the longest toe, the foot being pinned, sole downward, to a blackened board.

The statistical methods employed in analyzing these data have been rather fully discussed in a former paper (1915), to which the reader is referred.

(1) *Weight* and (2) *body length* are not dealt with directly in the present comparisons. The former is an index of metabolic condition as well as of size (*i. e.*, length). Captive mice, for example, are commonly fat in comparison with wild ones. *Body length* is of little significance in comparing two groups of mice, unless we know, either that the animals are all of the same age, or that the limit of growth has been reached by all of them. These things are frequently impossible to determine.

(3) *Tail length* is dealt with, both as an absolute value and as a percentage of the body length. If absolute tail lengths are to be compared in two groups of animals, the comparison can only be made between animals of approximately the same body length. My practise is to divide each series into a number of size-groups, differing by only two millimeters of body length. Group 80–81 of one series is then compared with group 80–81 of the other, group 82–83 with group 82–83, etc. The graphs (Figs. 6 and 7 and 9–12) are based upon this procedure. Each "curve" connects the means of the size-groups of each series of animals, the abscissas representing body length, the ordinates the character under comparison. In order to eliminate very young mice, groups having body lengths of less than 80 mm. are omitted. Even so, it is likely that most of the animals in the lower groups of the series are immature, but this fact in no way affects the validity of the comparisons.

It will be seen, from an inspection of the figures (6 and 7), for both males and females, that, as regards tail length, the Eureka mice (*rubidus*) stand in a class by themselves. In comparison with the wide interval between this long-tailed race and the other three races here considered, the latter differ but slightly among themselves. It is evident, none the less, that the La Jolla animals have somewhat longer tails than do those from Berkeley or Victorville, while the last two agree fairly closely in their mean condition.

Relative tail length, *i. e.*, the length of the tail expressed

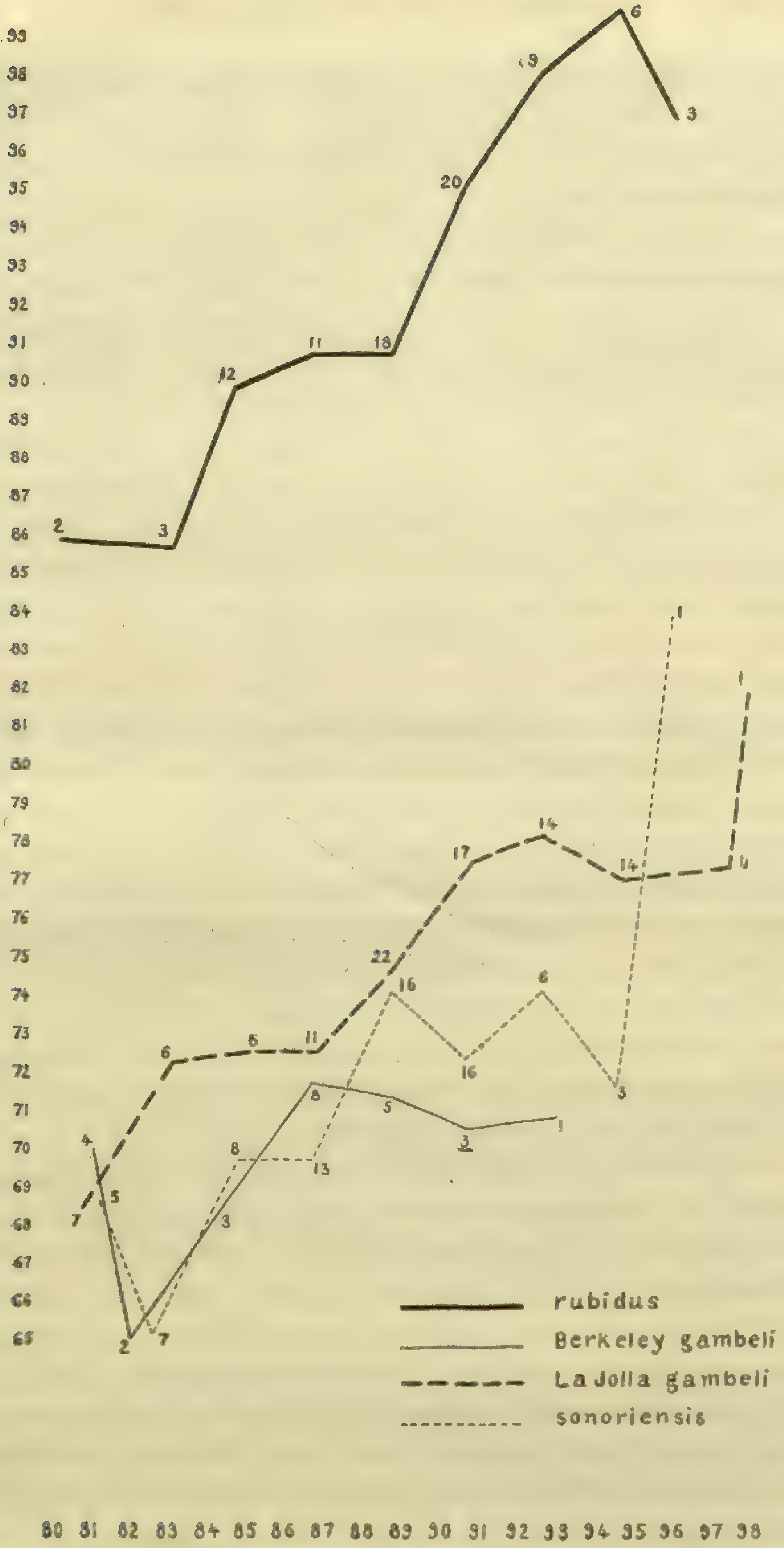

FIG. 6. Graphs for comparison of the absolute tail lengths in the four races (males). Abscissas denote body length; ordinates denote tail length; the figures along the "curves" indicate the numbers of individuals in the various size groups.

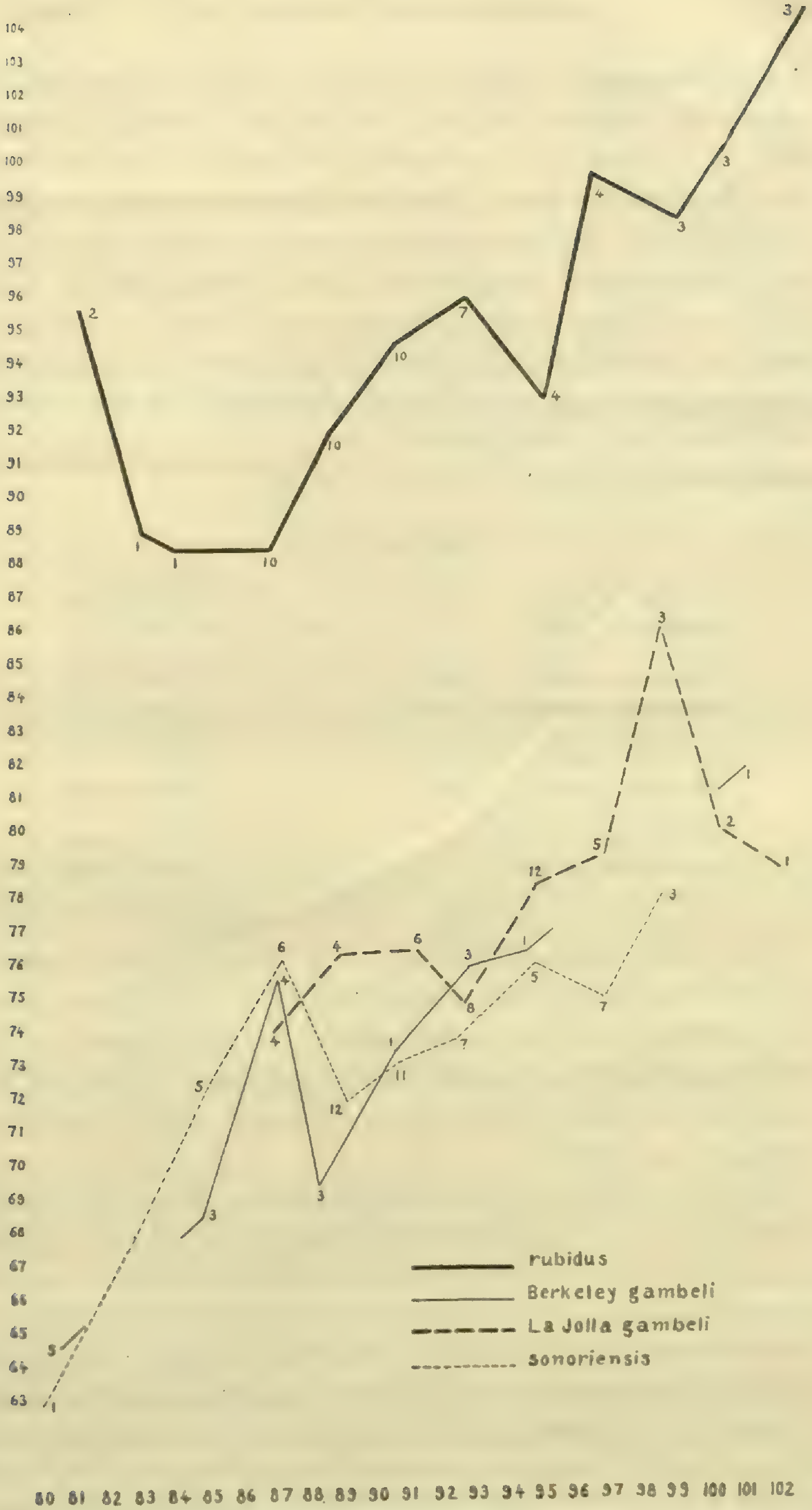

FIG. 7. Comparison of the absolute tall lengths in the four races (females).

as a percentage of that of the body, is to a considerable extent independent of the size of the animal. Larger mice, it is true, have relatively somewhat shorter tails than do smaller ones. But the differences are so slight that they may be overlooked, unless the mean size of the two groups under comparison differs considerably. The relative tail lengths of our four races of mice may be compared in the following table.[8] This shows the same relations as were portrayed by the graphs. It also shows that there are no significant differences between the sexes as regards the length of this member.

TABLE III

rubidus, ♂ (84)	104.45 ± 0.38
rubidus, ♀ (57)	103.37 ± 0.52
Berkeley *gambeli*, ♂ (26)	81.69 ± 0.55
Berkeley *gambeli*, ♀ (21)	81.76 ± 0.65
La Jolla *gambeli*, ♂ (99)	84.36 ± 0.35
La Jolla *gambeli*, ♀ (45)	83.04 ± 0.43
sonoriensis, ♂ (75)	81.29 ± 0.44
sonoriensis, ♀ (61)	81.30 ± 0.45

The distribution frequencies for these various lengths are represented by the histograms (Fig. 8). From these it is evident that only an occasional Eureka mouse has as short a tail as the longest tailed members of any of the other three races. The latter, however, differ from one another but slightly.

(4) In respect to *foot length* likewise (Figs. 9, 10) the Eureka mouse is very distinct from the other three races, while the latter show no significant differences among themselves. It is of interest, however, that in all four of these races the female has, on the average, a slightly shorter foot than the male. If any one still entertains the

[8] Owing to a slight change in the manner of measurement, which was made after these studies were commenced, the tail lengths of the earlier animals of my series have been rejected from the computations. This procedure has affected particularly the numbers of the Berkeley series.

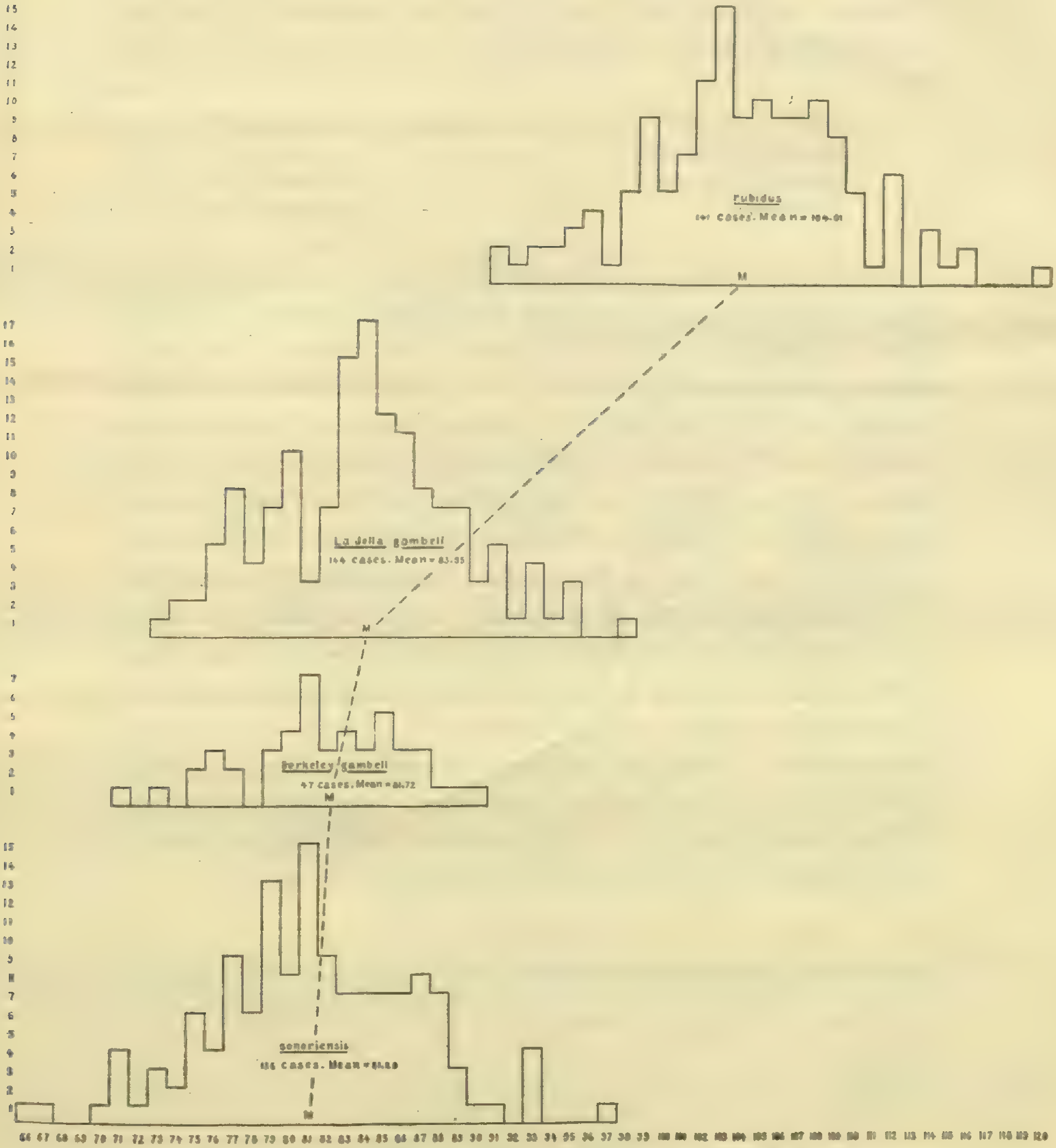

FIG. 8. Histograms, showing the frequency distributions of the percentage values for the length of the tail (ratio to body length), in the four races (sexes combined).

notion that small feet, along with other feminine charms in mankind, are due to "sexual selection," the situation in *Peromyscus* ought to give him pause.[9] The mean dif-

[9] This same difference was found by me to hold for white mice, at least for full grown individuals (1915, pp. 358, 367).

ferences between males and females, computed according to a method earlier described by me (1915, pp. 345, 346), are:

rubidus	0.31 mm. ± .08
gambeli (Berkeley)	0.29 mm. ± .05
gambeli (La Jolla)	0.09 mm. ± .07
sonoriensis	0.38 mm. ± .05

(5) In respect to *ear length,* we find a quite different set of relations. It is the La Jolla mouse in which these appendages are the longest, the Berkeley mouse in which they are the shortest, while the redwood and the desert animals occupy an approximately intermediate position and scarcely differ significantly from one another. It is here to be noted that the two extremes of the series, in respect to this character, have been placed by the systematists in the same "subspecies" (*gambeli*).

(6) The counting of the *tail vertebræ,* like the other measurements of skeletal characters, has not yet been completed. I have, however, determined the number in 25 specimens each of the Eureka, La Jolla and Victorville races. The fifth vertebra, counting from the most anterior one in the sacrum, has been regarded as the first of the caudal series. The averages and the frequency distributions are indicated in the following table.

TABLE IV

	23	24	25	26	27	28	29	30	31	Average
rubidus				2	9	6	5	1	2	28.0
gambeli (La Jolla)			4	5	13	3				26.6
sonoriensis	1	2	8	7	6	1				25.7

The significance of these differences seems highly probable, despite the small numbers. That between *rubidus* and *sonoriensis* can hardly be questioned. It seems plain, however, that the differences in tail length between these various races is not accounted for by the differences in the number of the vertebræ. Thus the Eureka mouse has a mean tail length which is 28 per cent. (of the smaller number) longer than that of the desert mouse. The pre-

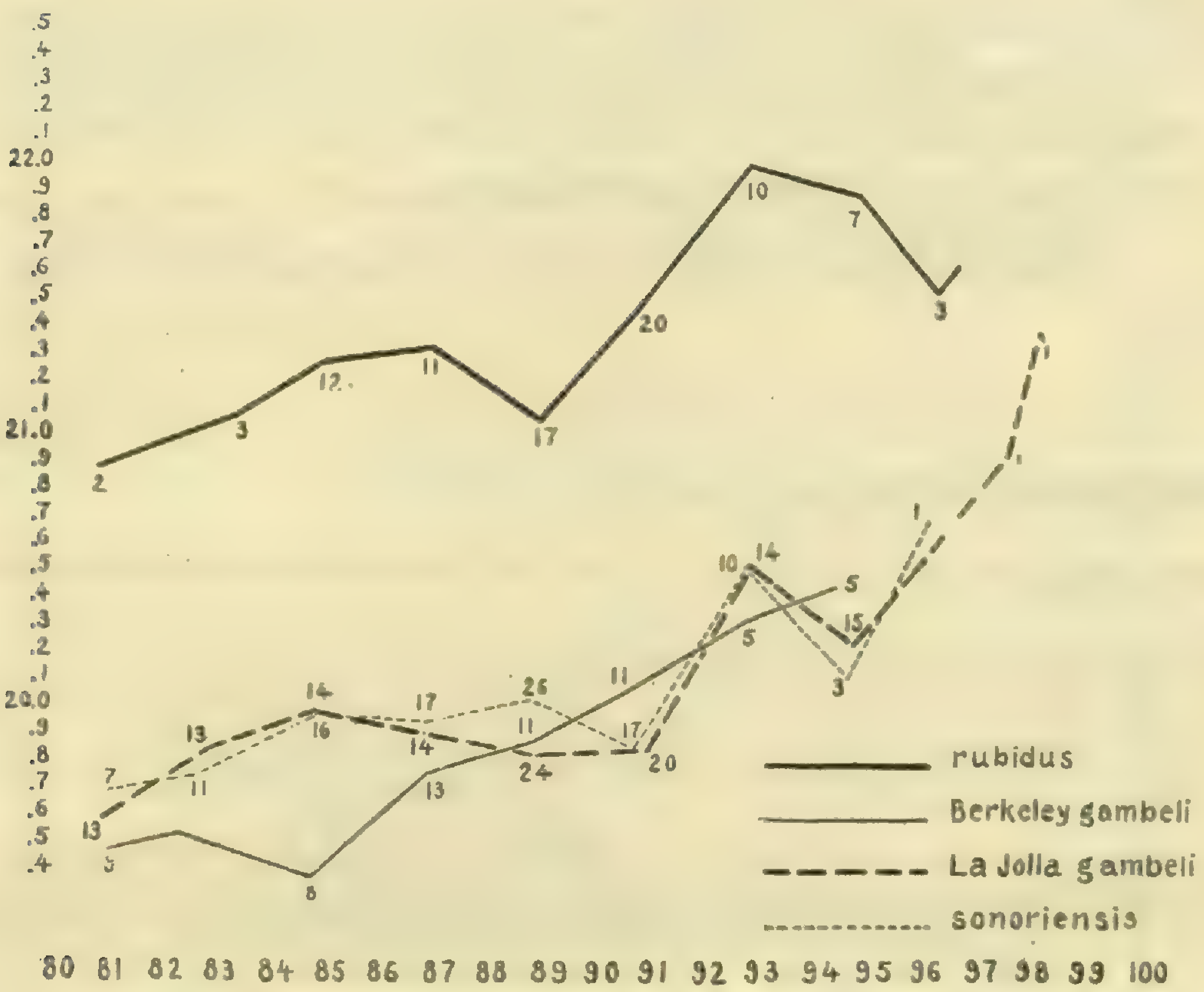

FIG. 9. Comparison of foot-lengths in the four races (males).

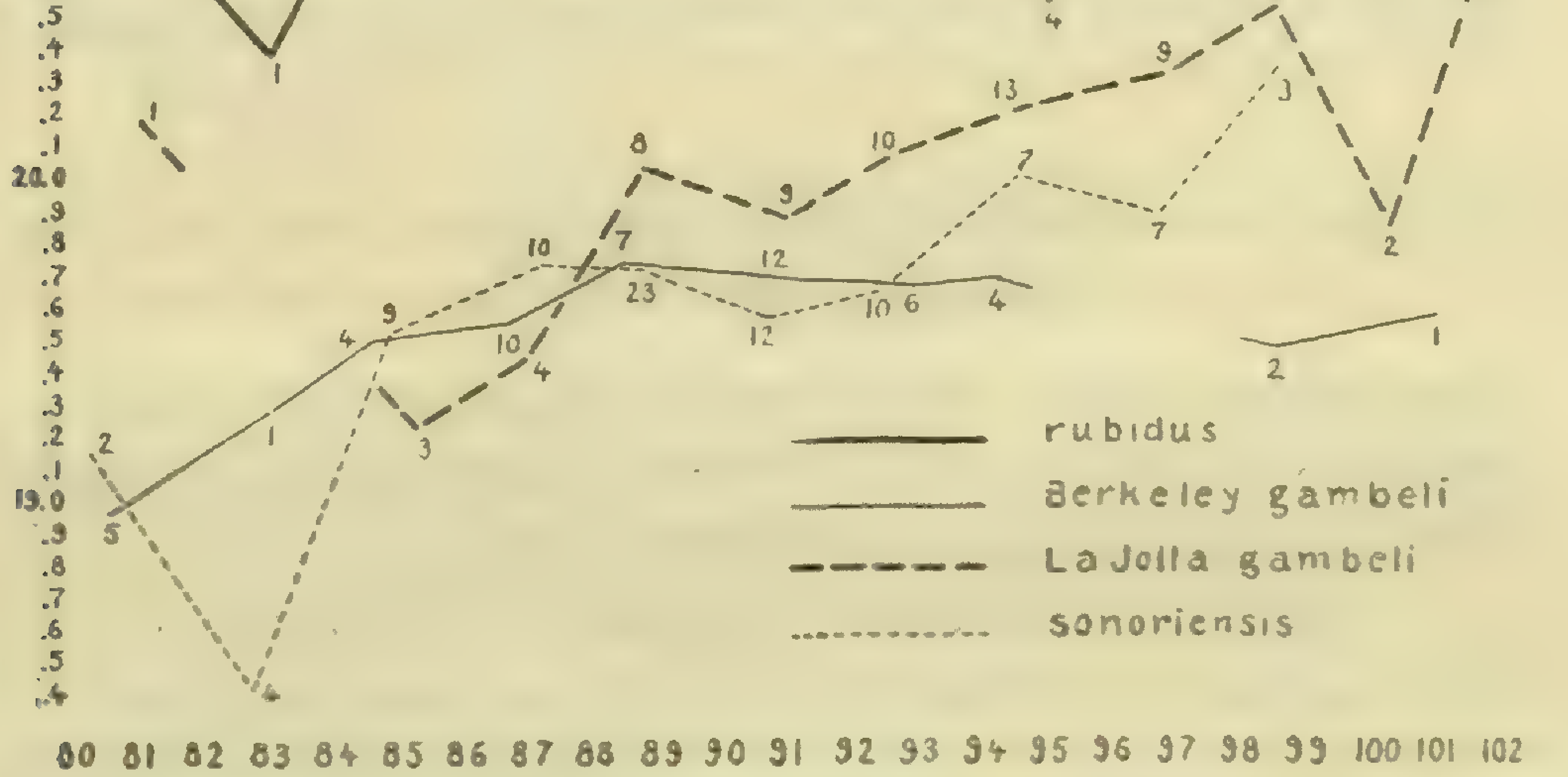

FIG. 10. Comparison of foot-lengths in the four races (females).

ponderance in the number of vertebræ is only 9 per cent. The differences in the length of this appendage are therefore due partly to the number of vertebræ, but chiefly to the length of the individual vertebræ.

Résumé of Racial Differences.—In relation to the vari-

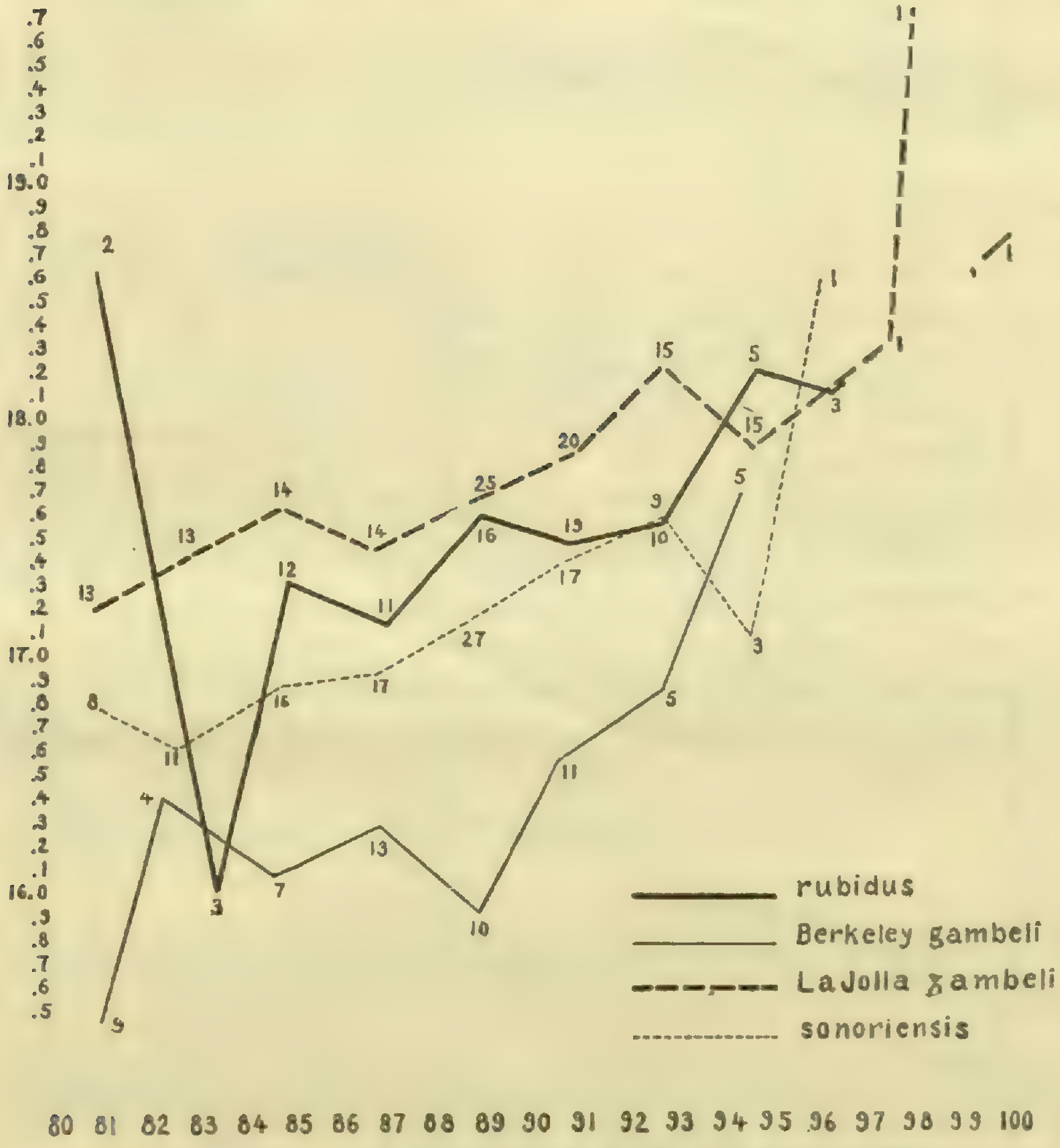

FIG. 11. Comparison of ear-lengths in the four races (males).

ous pigmental differences, those both of intensity and extensity, the four races under consideration were found to present the following graduated series:

Eureka > Berkeley > La Jolla > Victorville.

As regards the length to the tail, the series became:

Eureka > La Jolla > { Berkeley, Victorville.

When the number of caudal vertebræ was considered, we had the same arrangement as the last for the three races for which determinations had been made, viz.:

Eureka > La Jolla > Victorville.

In respect to foot length, the following order held:

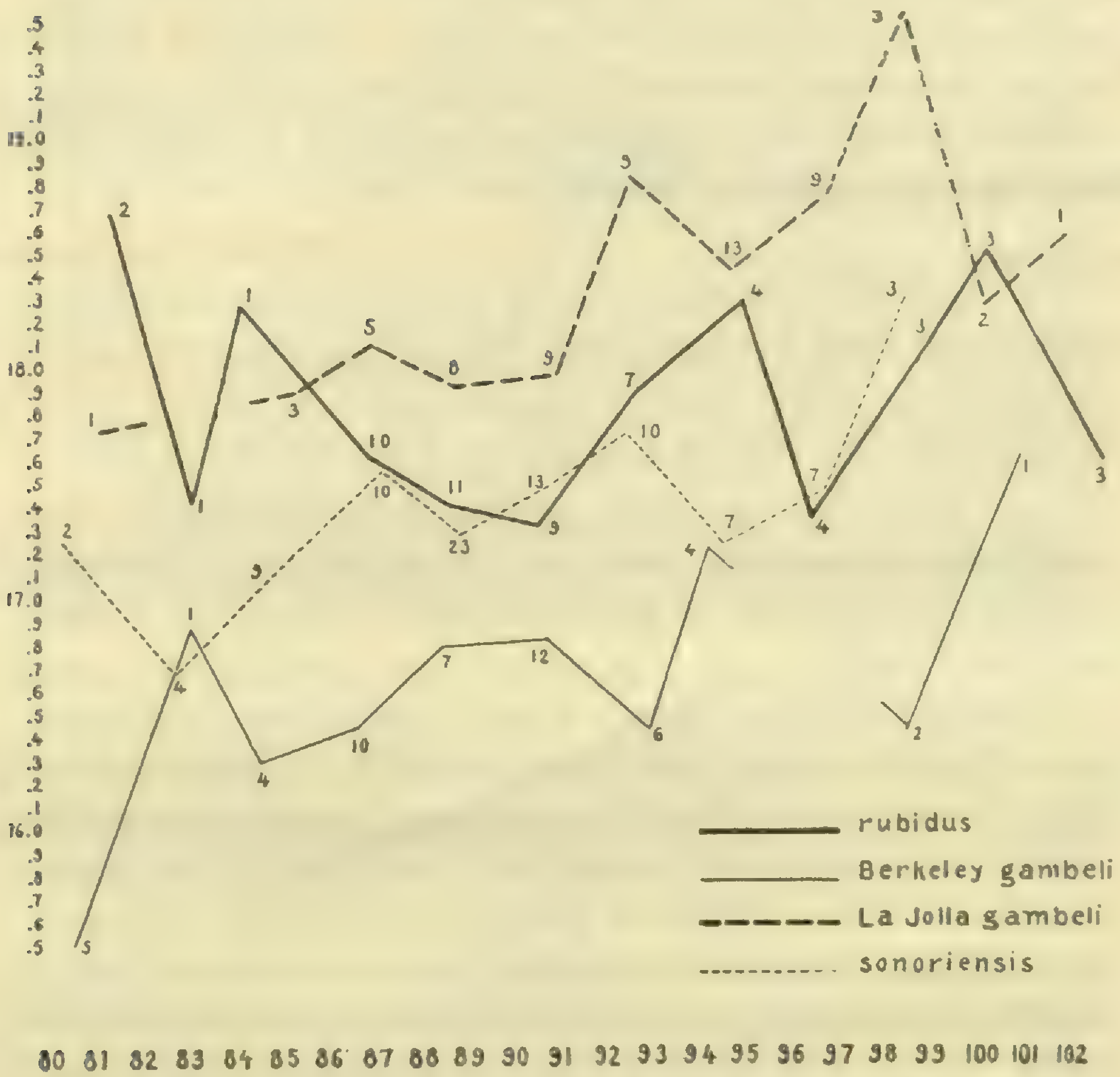

FIG. 12. Comparison of ear-lengths in the four races (females).

$$\text{Eureka} > \left\{\begin{array}{l}\text{La Jolla,}\\ \text{Berkeley,}\\ \text{Victorville.}\end{array}\right.$$

Finally, as regards ear length, we had a quite different alignment, viz.:

$$\text{La Jolla} > \left\{\begin{array}{l}\text{Eureka}\\ \text{Victorville}\end{array}\right\} > \text{Berkeley.}$$

It is plain that these "subspecies" have diverged from one another in respect to characters which have varied

quite independently. There is no single graded series for all the characters, which would lead us to suppose that they are in some way correlated or "linked" together.

When pigment characters alone are considered, the Berkeley mice are certainly intermediate between the La Jolla and the Eureka ones, and to that extent may be said to "approach *rubidus*."[10] But this is not true of the length of the tail, the foot or the ear. Indeed, as regards the first of these appendages, the Berkeley race diverges even farther from the Eureka race than does that of La Jolla.[11]

The question whether any of these various character differences may be physiologically or genetically linked together, so as to exhibit concomitant variations, is an interesting one, which I hope, in time, to treat rather fully. But I have already computed coefficients of correlation between two pairs of characters, viz.: between tail length and width of tail stripe, and between tail length and foot length.

In obtaining the former, I have based the coefficients upon the deviations from the mean *relative* tail length of each race and each sex, taken separately. Of these coefficients, three are positive and five negative. They range from -0.23 to $+0.09$, the mean being -0.03. Thus, it is plain that there is no appreciable correlation, within a single race, between the width of the tail stripe and the length of the tail, despite the fact that these characters seem to be associated, when certain darker races of the northwest coast are compared with more southward ranging forms.

There is, however, a quite marked correlation between the length of the tail and that of the foot. I do not here refer to the obvious fact that larger animals have larger

[10] Osgood, 1909, p. 69. This author likewise states that Berkeley specimens are "longer-tailed than typical *gambeli*."

[11] This conclusion is strengthened by consideration of an even larger series of Berkeley mice which were not included in Table III. The two sets were trapped in two different localities in the Berkeley hills.

tails and likewise larger feet than smaller animals. My figures show that, *even when animals of the same body length are considered,* those with longer tails tend, on the whole, to have longer feet, and vice versa. To obtain these results, I have computed the coefficients separately for each size-group, containing ten or more individuals.[12] All but 5 of these 21 figures are positive, the mean being +0.27. Thus the greater tail and foot length of the Eureka race may have arisen simultaneously, both being the expression of a single constitutional change.

One further word regarding the nature of these racial differences, before we pass to a consideration of their heredity. It is plain that, with a single possible exception, all of the differences thus far considered are "substantive," rather than "meristic," to follow Bateson's[13] terminology, or "proportional," rather than "numerical," to use terms recently employed by Osborn.[14] In no case are they of the nature of "presence-and-absence" differences, such as figure so widely in Mendelian literature. Whether or not, on ultimate analysis, they can be resolved into the latter category, will be discussed later.

The differences without exception relate to means and modes, as was illustrated above by histograms constructed for two of the characters (Figs. 5 and 8). The frequency polygons commonly overlap broadly, when adjacent members of the series are compared. We find an approach to discontinuity only in a comparison of the most widely divergent races.

The single difference of a meristic or numerical character is that relating to the number of caudal vertebræ. But even here the difference is one of averages, for no single race seems to be characterized by the unvarying presence of any particular number of vertebræ, as certain larger taxonomic groups are characterized by a definite number of teeth or mammæ. It is worth mention also that

12 Cf. Sumner, 1915, pp. 349–350, 409–415.

13 1894, pp. 22, 23.

14 1915, p. 199. In the paper referred to, Osborn has given some attention to the case of *Peromyscus.*

the last one or two caudal vertebræ are commonly rudimentary, so much so that it is not always easy to determine their exact number. It is scarcely more fitting to apply the term "meristic variation" here than it would be to apply this term to such variations in the number of cells as distinguish a larger from a smaller foot or ear.

(To be concluded.)

INTERNAL FACTORS INFLUENCING EGG PRODUCTION IN THE RHODE ISLAND RED BREED OF DOMESTIC FOWL II.

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Cycles.—By cycles of egg production are understood the existence of periods of egg production alternating with periods either of decreased egg production or entire cessation of egg production. These cycles may be either long or short. The long-term cycles may have a period of a year. Shorter cycles exist with a period of three or four months, *i. e.*, winter, spring and summer and fall. There are still shorter cycles with periods measured in weeks, while one may also recognize irregular cycles. A litter, as defined by Miss Curtis ('14), is a short period of egg production alternating with a non-productive period and is well illustrated by broody birds, though it may occur in non-broody individuals. A "clutch," according to Miss Curtis, is the set of eggs produced on consecutive days. Its termination is marked by the appearance of a blank day.

The form of the yearly cycle depends to a considerable degree upon some of the internal factors under discussion, that is, it varies in different individuals. Egg production, as a rule, begins in the fall and winter, and continues at a fairly constant rate in most individuals until spring, when the rate rises somewhat in many individuals. Those that have been laying at a relatively high rate do not show this acceleration, at least not in as marked a degree. Sooner or later in a broody race broody periods appear, which interrupt egg production at fairly constant intervals. The rate, however, during the nonbroody periods shows no slackening, but on the contrary a very slight acceleration may be demonstrated, so

that the lower egg production noted after the first broody period is due solely to the interruption of production. During the summer, the rate of egg production slackens, due almost entirely to the broody periods. The data for the 1913–14 flocks show that after June the rate of production is about constant for the next three months, largely because the first of July marks the point at which practically every individual in the flock has entered on its broody portion of the year. Some time in the late summer or during the fall, the various individuals stop laying and moult, some at one time, some at another, but usually at the end of a broody period. After the rest period in the fall, the birds gradually begin to lay again in mid-winter, somewhat as they did as pullets, except that the rate is slower as a rule. Except for this feature, the character of the second year's production is much the same as the first.

The winter cycle is regarded by the workers at the Maine Station (Pearl, '12) as the most important of all the cycles, at least from the standpoint of the investigation of the inheritance of egg production. They have found that it represents a definite period in the life history of the individual, among their Barred Plymouth Rocks. Furthermore, during this period, the greatest differences are to be observed in the egg production among individuals. They also find that high winter egg production is correlated with annual egg production, as would be expected except in the event that high egg production early in life tends to lower production in later life. In other words, a bird that is a good layer during the winter is probably a good layer at all times. There are other reasons, mostly of a practical nature for the use of the winter cycle as a measure of fecundity.

Taking the year as a basis the workers at the Maine Station recognize as its first characteristic the winter cycle beginning with the first egg of the pullet and extending to March 1. This date is taken as a convenient working point that falls near the biological division point.

During this period, flock production rises from zero to a maximum and then slows down somewhat toward its close. This slackening is due to a cessation of production on the part of most individuals while nearly all show at least a slackening of egg production towards the close of the winter cycle. The exact date at which the cycle ends varies with the individual, and may occur at almost any point during the winter months including March. Miss Curtis ('14), in another connection, has published the monthly records of a few hens that show this cycle. They are shown in Table VII. With one exception, No.

TABLE VII

A Portion of Table XXV from Curtis ('14) Showing the Winter Egg Production of a Number of Barred Plymouth Rock Pullets. The Decreased Production in January and February over the December Records in Nine Instances is Evidence of a Winter Cycle.

Month	Pullet Number												
	218	139	446	516	192	259	204	478	212	184	211	236	441
1910													
October	...	3	...	...	...	...	...	...	...	...	...	...	...
November	15	19	17	15	18	8	5	13	6	12	8	1	9
December	25	18	27	24	24	11	16	24	8	14	15	0	18
1911													
January	13	19	6	9	14	13	4	10	11	6	5	0	14
February	13	10	15	9	0	16	13	0	8	11	5	0	16
Winter total	66	69	65	57	56	48	38	47	33	43	33	1	57

236, the birds all laid over 30 eggs. The evidence for a winter cycle is shown by the depressed egg production in January and February and is very clear. The records published by Gowell, '02, '03, also show this point.

Pearl and Surface, '11, describe the other periods as follows:

The next period (March, April and May) is the natural laying season. It corresponds to the egg-laying part of the natural reproductive cycle exhibited by the wild *Gallus*. . . . Naturally, therefore, a high mean and a low variability in production are exactly what we find characterizing the laying in each of the months of this period.

The third period (June, July and August) is characterized by a gradually falling mean production and a variability gradually increas-

ing. . . . This is the period in which the rearing of the chickens naturally occurs and it also represents an extension of the breeding season.

The fourth period (September and October) is not easily separated from the third in respect to laying, but in general it is the period of moulting. . . . It is characterized by reduced laying and marked increased variability.

It is not clear from their accounts whether or not they consider that these periods extend through the second year or whether they are to be considered as characteristic solely of the pullet year.

Just how far the data on Barred Plymouth Rocks are applicable to our Rhode Island Reds is somewhat uncertain. At the outset it is evident that the small percentage of birds that show an interruption in their winter laying because of the presence of a broody period afford no evidence either for or against the existence of a winter cycle. Of the birds that do not go broody during the winter two classes can be distinguished, viz., those that show an interruption in their winter laying and those that do not. In the 1913–14 flock and in the 1915–16 flock from the original source, a large percentage of the birds show no interruption in production, not even a slump in the rate of production. Such birds lay at an approximately constant rate through the late fall and winter months, and on through the spring. Among the records of the main portion of the 1915–16 flock are many that show an interruption or else a slackening of production. Of these birds it can be said that they have a winter cycle. But there are two points about these records that make it difficult to interpret the interruption in production as an index of a cycle. First, the interruption may occur at almost any time during the winter followed by a resumption of production in mid-winter, and second, some individuals show more than one period of nonproduction. While there is definite evidence that a winter cycle exists in *some but not all* Rhode Island Reds, the possibility that some at least of these interruptions of production may be due to environmental factors must be fully recognized.

As already noted, there are many Rhode Island Reds which show no sign of a winter cycle. Whether this means that such birds do not have a winter cycle, or whether it means that some other factor covers up an underlying cycle is uncertain. In many instances these birds are very much like the Barred Plymouth Rocks noted by Pearl and Surface, '11, who state:

> Many birds of course have no proper winter cycle at all. They begin to lay for the first time in January or February and keep on laying without any large break straight through the spring cycle.

But there are many other Rhode Island Reds that begin to lay in October, November and December and lay through the winter and spring without any breaks whatsoever. Moreover, those birds that begin to lay in January or February for the first time very rarely show any break whatsoever. For these instances where the birds begin to lay late in the winter it is conceivable that the winter cycle might extend well into March but that the comparatively mild weather at that season of the year would tend to eliminate the rest period and thus conceal the winter cycle. But this argument cannot be applied to those instances in which the laying is continuous from its start in October, November or December right through the spring. There seems no reason to speak of a winter cycle for this class of Rhode Island Reds.[4]

The spring cycle, in Rhode Island Reds, in so far as it can be differentiated from the winter period, differs chiefly from that of the Barred Rocks in extending nearly through June, since the end of June marks the point at which practically every bird that will go broody has become broody at least once. Egg production is at its maximum at the beginning of this period due to active laying on the part of practically all individuals but falls sharply

[4] Later work on this point demonstrates, beyond doubt, that the presence of a definite winter cycle is not characteristic of our strain of Rhode Island Reds as a whole. There is some evidence, moreover, that the winter cycle is a Mendelian recessive, the dominant allelomorph being continuous winter production. For details see Goodale, '18.

after its middle, the rate of decline being much greater than for the Barred Plymouth Rocks.

The summer period may be considered to be July, August and September. Practically all the birds of the flock are laying in broody cycles with egg production remaining at approximately a constant level, while considerable partial moulting is going on. It passes gradually into the fall period which is characterized chiefly by the cessation of egg production—usually coinciding with a broody period—and the onset of the fall moult together with some slowing in rate of production of those birds that are laying. Biologically the fall period overlaps the calendar year since it may extend into December. The question of egg production in the fall, at the end of the pullet year, is on rather a different basis from that of the other seasons of the year. The egg producing mechanism of the hen seems to be in a peculiarly unstable condition and unless great care is exercised may cease functioning in response to slight adversities in environment. Some hens, however, and this is really the important point, continue to lay throughout the fall months with the same regularity they exhibited in the spring. This affords us an opportunity to build up a strain of birds that will be persistent layers throughout the year.

Thus, persistency in egg production through the fall months enters in as a factor in determining the total egg production as has also been emphasized by Rice ('14). Some birds cease laying relatively early in the fall, say late in August or September; others, however, of the same age, breeding, and under the same conditions, continue to lay all through the fall, at approximately the same rate of production as during the summer months, although the rate may fall off slightly. Now, these birds will have quite a different total record from those that stop early in the season and if one examines his records he finds that while many persistent layers are also good producers early in the season, nevertheless a great many of the birds that were good layers during the winter are

not persistent layers during the fall, while some birds with low winter records are good fall layers.

Other kinds of cycles, which are described in the following paragraphs, have been noted in the Rhode Island Reds. In broody individuals, where the practice is followed of "breaking up" the hen, a series of cycles is introduced, marked by broody periods alternating with an egg production period. If the natural course of events is not interfered with in the case of broody hens, the broody period lasts until the chicks have hatched. Then the period of rearing takes place. Toward the end of this period the hen begins to lay and the cycle is repeated.

There is also a short time cycle of one or two weeks which needs little discussion at present. It is shown by an acceleration in rate of egg production followed by a decline somewhat as follows: Egg—blank—egg—egg—blank—egg—egg—egg—blank—egg—egg—egg—egg—blank—egg—egg—egg—egg—blank—egg—egg—egg—blank—egg—egg—blank—egg—blank—egg—blank—egg—blank—and repeat. Although one often finds records that approximate closely the above scheme, their rarity suggests either that the fluctuations in rate are due directly to some extraneous circumstance or, if there is a fundamental rhythm of this sort, that it is subject to disturbance from the environment. Whatever may be the cause, at present it is doubtful if it is indicative of an internal factor.

The next type of cycle is that exhibited by certain hens which lay at a relatively high rate for a time and then stop. This period may correspond to the term often used by poultrymen when speaking of a hen's clutch. Here again we are confronted by doubt as to the causation of these blanks, for many hens do not have such pauses in production. Once they begin laying they continue without any considerable vacant period (not exceeding three or four days) until the onset of the first broody period.

Stamina.—A strong bird is readily distinguished from a weak one, but it is difficult to separate the birds per-

manently according to a definite standard since it is impossible to secure a constant environment. A fairly uniform environment in the sense that all birds are exposed to the same external conditions at any one moment is fairly easily secured; but since the external conditions, particularly weather conditions, are very variable and follow no definite course, and since a bird's vigor is a resultant of its own inherent strength of resistance against the environment, it is clear that the objective vitality observed in each member of a flock may be unequally affected by the surroundings.

The evidence available on the relation of vitality to fecundity thus far points in two more or less opposite directions. Many birds of low vitality have made not only excellent but even high records. On the other hand, birds of strong vitality may make low records. At the same time there is a point at which the vitality becomes too low for good egg production. In the fall of 1913, thirty-eight birds graded early in the fall, before laying commenced, as "poor" in respect to vigor, were put in the laying houses. They had an average record for the winter period of only 20 eggs against an average of 38 for the entire flock, including the poor birds. Low vitality evidently depressed egg production in this instance; mainly, through retardation of the time of commencement of laying rather than by slow production. The influence of lack of vigor on winter egg production is shown in Fig. 9, where the curve of winter egg production for the entire flock is represented by the continuous line and that for the "poor" birds by the dotted line.

Occasionally, birds of low vitality may make excellent egg records. In one family in particular, the birds were of distinctly mediocre quality, as evidenced by their weight, activity, hatching quality of eggs and viability of chicks and yet they were able to make high records, the average for the family of seven individuals being 63.3—ranging from 33 to 81—for the winter period, with a yearly average of 192.4 for the five birds that survived throughout the year, and with a range of 154 to 210.

Moult.—Moulting exercises some influence on the number of eggs produced, since birds that are moulting often do not lay, particularly during the fall moult. Moulting itself may be induced at certain seasons of the year by changes in management, especially those changes that tend to stop egg production. Such changes apparently change the course of the metabolism of the bird. Broodiness in late summer and early fall appears to be a common cause of the onset of a moult and consequent cessa-

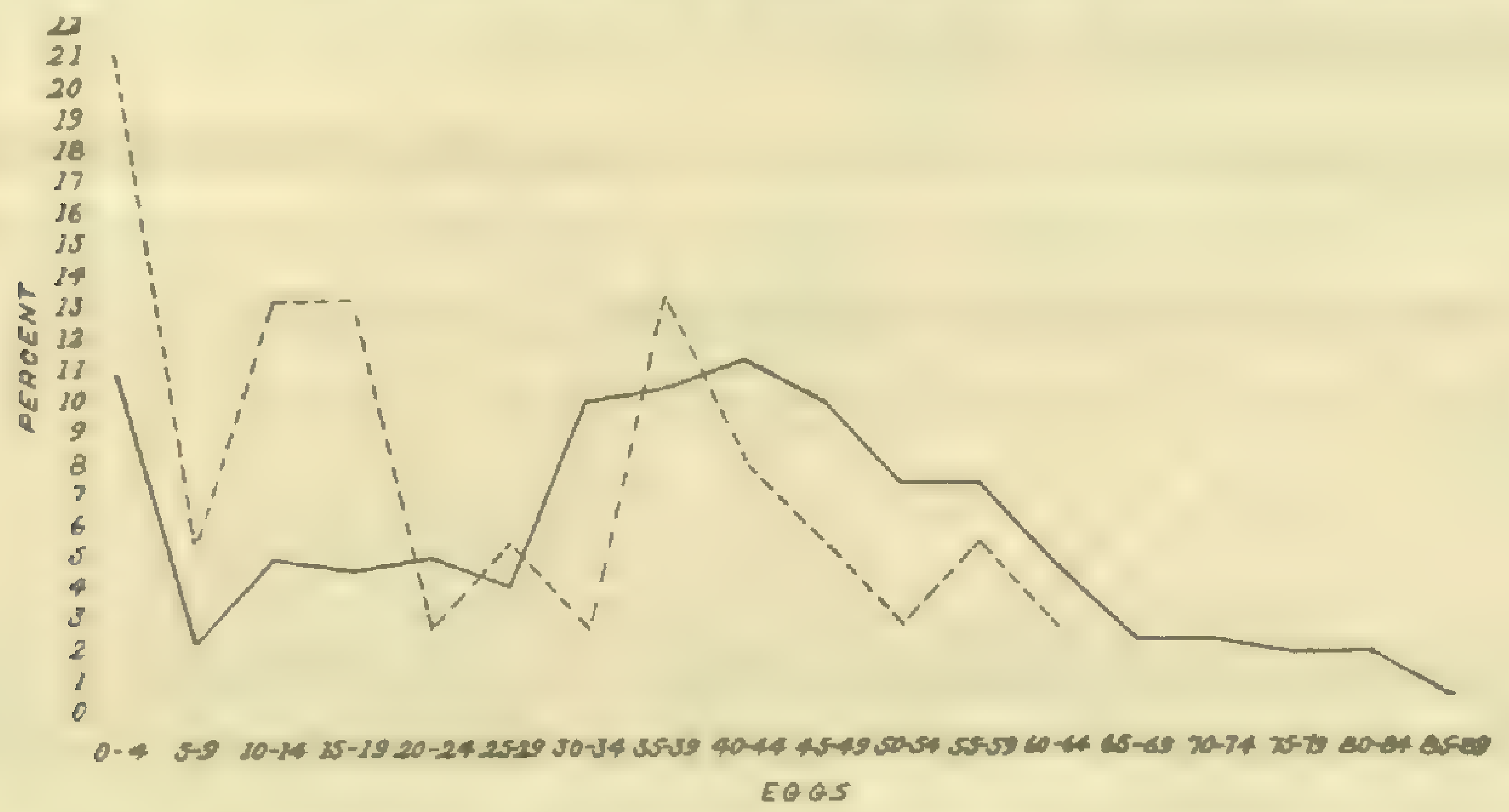

FIG. 9. The effect of low vitality on winter egg production. The graph shows the percentage of the flock of 1915–16 laying the specified number of eggs. The continuous line is for the entire flock. The dotted line is for that portion of the flock graded "poor" or of low vitality, before being placed in the laying houses.

tion of egg production. At least one might draw this conclusion from the fact that egg production, as the usual rule, ceases with a broody period, for in most instances the last egg laid in late summer or early fall coincides with the beginning of a broody period. It is not clear, however, whether the moult starts because the bird has reached the limit of her production period, or whether the moult begins because of the interruption to egg production due to the onset of the broody period.

In the Rhode Island Reds we have observed a partial moult that begins in the early part of the summer and as a rule seems to affect egg production very little. In the autumn this partial moult is followed by a more extensive (often complete) moult attended by cessation of production. It is possible that the summer moult has been in-

duced by broodiness, but that the hens are broken up so quickly and the impulse toward resumption of egg production at this season is so strong that it inhibits the moult at various stages.

Pullets that begin to lay very early in the fall very often undergo a moult during the latter part of the same fall. It is not clear that early production of itself tends to induce the moult so long as the birds affected are not hatched too early in the season. The moult is more commonly observed in pullets that are hatched very early in the season and which begin to lay in August and September. Such birds rarely make a continuous record but instead stop laying after producing a variable number of eggs and moult much like birds from fifteen to eighteen months of age. In the flocks with which we have been dealing the variability in maturity has induced some complications in handling the flocks. If an attempt is made to hatch birds sufficiently early in the season, so that a good share of them will begin laying in November, some begin too early, lay a while, and then moult.

Rate and Rhythm of Production.—The percentage rate of production at any time and for any period may be taken as the number of eggs times 100, divided by the length of the period involved, measured in days. Rate is an important factor in determining egg production, but in the Rhode Island Reds is of quite secondary importance as compared to date of first egg (and of course age at first egg).

The distribution of the percentage rate calculated for the winter period (between the first egg of each pullet and March 1) for the flock of 1913–14 has been determined and the graph shown in Fig. 10 plotted. The curve shows a considerable homogeneity of rate in the flock. Since the general trend of events, such as accidents, temporary ailments, etc., is of such a nature that some birds do not attain their natural inherent rate, the curve shows a very gradual slope at the left-hand side up to about 30 per cent., a somewhat more rapid rise be-

tween 30 and 50 per cent. and a much sharper rise beyond 50 per cent. The mode comes at the 61 to 70 per cent. group, while the maximum rate does not exceed 90 per cent. It is interesting to note that 8.5 per cent. of the

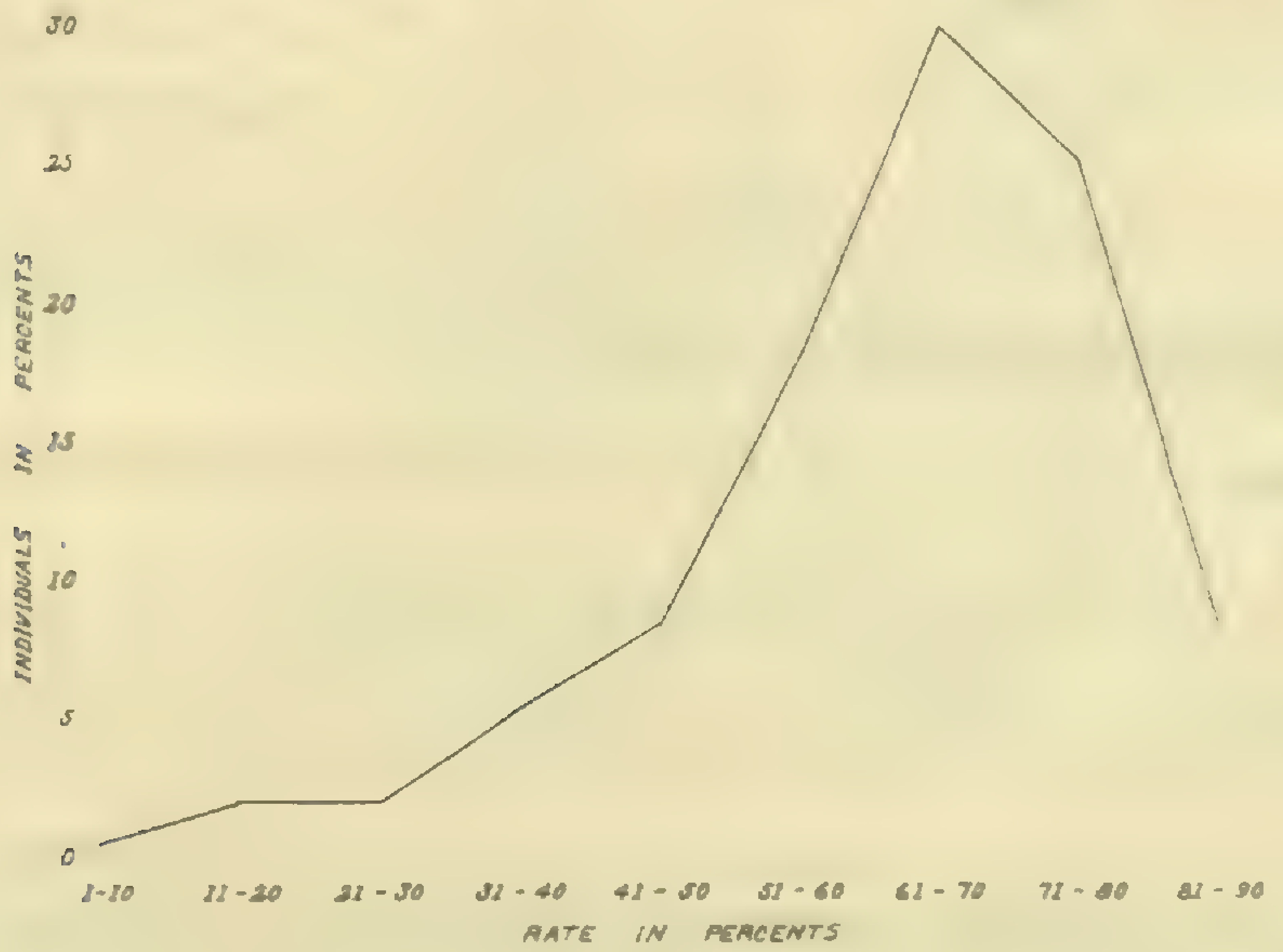

FIG. 10. Percentage rate of production for the winter period. The percentage of the flock laying at the specified rate is shown by the ordinates, the rate by the abscissæ. Flock of 1913–14. M = 62.50, S. D. = 15.77, C. V. = 25.23.

flock laid at a rate exceeding 80 per cent. for the entire winter period.

The effect of variability in rate on total production for a definite period is shown by the records given in Fig. 11.

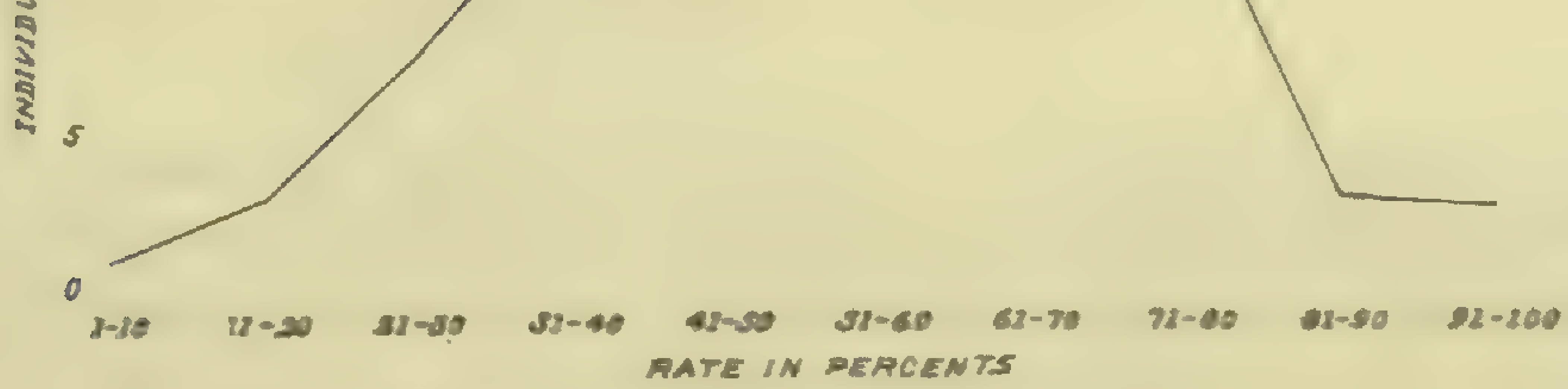

FIG. 10*a*. Percentage rate of production for the winter period. The percentage of the flock laying at the specified rate is shown by the ordinates, the rate by the abscissæ. Flock of 1915–16. M = 54.59, S. D. = 18.52, C. V. = 33.93.

No. 49 HATCHED MARCH 16, 1913. AGE AT FIRST EGG, 248 DAYS

Date 1913-14	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Nov.																			/	/	/		/	/	/	/	/		/	/	■	10	
Dec.	/	/		/	/	/	/		/	/	/	/	/	/	/		/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	28	
Jan.	/	/	/		/		N	/		/	/	/	/	/	/		/	/	/	/	/	/	/	/	/	/		/	/	/	/	25	
Feb.	/	/	N	/	/	/	/	/		/	/	/	/	/	/	/	/	/	/	/	/	/	/	/		/	/	/	■	■	■	25	88
Mar.	/	/	/	/	/		/		/	/	/	/	/	/	/	/		/	/	/	/	/	/	/	/	/	/	/	/	/	/	28	
Apr.	/		B L			A	N	N	N	N N	N N	N BL		A N	/	/	/	N	/	/	/		/	/	/	/	/	/	/		■	14	

No. 4797 HATCHED MARCH 21, 1915. AGE AT FIRST EGG, 236 DAYS

Date 1915-16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Nov.												/		/		/	/		/	/		/	/		/	/		/	/		■	12	
Dec.	/		/	/		/	/		/		/	/		/		/	/		/		/		/		/	/		/	/		/	19	
Jan.	/		/		/		/		/		/		/		/		/		/		/		/			/		/		/		15	
Feb.	/		/		/		/		/		/	/	/	/		/	/		/		/		/	/		/	/		/	■	■	18	64
Mar.	/		/	/		/	/		/	/		/	/	/		/	/	/		/	/	/		/	/	/	/		/	/	/	23	
Apr.	/		/	/	/		/	/		/	/	/		/	/	/	/		/	/	/	/		/	/	/	/	/		/	■	23	

FIG. 11. Types of daily egg records with special reference to the winter egg production, although the records for March and April are also shown. All three pullets matured near the average age. No. 49 is that of a pullet that laid continuously at a high rate. No. 4797 is that of a pullet that laid continuously at a rather slow rate of production, while No. 5080 is a pullet that laid intermittently and at a slow rate. This last would seem to be a mediocre producer in Pearl's sense.

Number 49 laid at an exceptionally high rate. On the other hand No. 4797 laid at a rather low rate for a bird that produced eggs continually throughout the winter. Although she began laying several days earlier in the year than No. 49, she produced 24 eggs less, due to her slow but steady rate of production. An entirely different type of rate is shown by No. 5080. This bird is a true mediocre producer in so far as may be judged from her record. She laid her first egg at a fairly early date and fairly early in the season but her rate of production was very low. The eggs, too, were produced at haphazard intervals. Her record is to be compared with that of No. 4568 (Fig. 4), which laid the same number of eggs but all in the last part of February. Records similar to those of No. 5080 are shown by Nos. 274 and 280 (Fig. 12), both Barred Plymouth Rocks in one of the contest pens at the Essex County Agricultural School. Another type of rate is shown by No. 4815 (also Fig. 12), which exhibits also a well-defined winter cycle. This bird matured early, began laying early in the season, and laid well for about six weeks. Then she stopped entirely and did not lay at all again until late in February.

While rate may be considered independently of the rhythm, *i. e.*, rhythm may be ignored; rhythm can not be considered apart from rate. A hen may lay twelve eggs in a month and the rate be described as such or as 40 per cent. without paying any attention to the sequence in which the eggs appear, but if the rhythm be considered, attention must be paid to the sequence between eggs. Thus, two blank days may repeatedly alternate with one blank day between eggs, producing a regular rhythm, or the twelve eggs may be laid in groups of two, three, or more eggs on successive days and then a considerable period of blank days intervene, the rhythm in this instance being irregular. A certain degree of regularity of rhythm is closely associated with high rate of production, though some birds of relatively low rate lay in a regular rhythm (Fig. 11). Most low-record birds, how-

No. 5080 HATCHED MARCH 28, 1915. AGE AT FIRST EGG, 244 DAYS

Date 1915–16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Nov.																										N	/				■	1	
Dec.																				/					/		/		/			4	
Jan.																																0	
Feb.												N	NN		/		/		/		/		/	/		/				■	■	7	12
Mar.	/		/		/		/						/		/		/		/		/	/		/		/		/		/		14	
Apr.	/	/		/	/		/		/	/		/	/		/	/		/	/		/	/		/	/		/	/	/		■	20	

FIG. 11. (*Concluded.*)

No. 274 HATCHED 1915. AGE AT FIRST EGG, UNKNOWN

Date 1915–16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Nov.																															■	0	
Dec.			/		/				/																	/		/				5	
Jan.															/									/			/					3	
Feb.			/				/																				/	/	/	■	■	5	13
Mar.	/																								/		/	/				4	
Apr.		/	/					/	/	/	/			/	/		/	/	/		/	/	/			/			/	/	■	17	

FIG. 12. Daily records of two Barred Plymouth Rocks (Nos. 274 and 284) in the contest conducted by the Essex County (Mass.) Agricultural School. They are mediocre producers. The third record, *i. e.*, of 4815, a Rhode Island Red, shows a long winter rest period, *i. e.*, a winter cycle.

No. 284 HATCHED 1915. AGE AT FIRST EGG, UNKNOWN

Date 1915–16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Nov.......																															■	0	
Dec.......														/		/			/													3	
Jan.......																/		/	/	/	/	/	/		/	/	/	/	/	/	/	14	
Feb.......			/				/	/																	/					■	■	4	21
....							/		/	/	/		/	/	/	/		/	/		/	/		/	/		/					15	
Apr.......				/		/				/		/	/	/	/		/										/		/	/	■	11	

No. 4815 HATCHED MARCH 21, 1915. AGE AT FIRST EGG, 227 DAYS

Date 1915–16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Nov.......			/		N	/		/	/	/	/		/	/	/	/	/		/	/	/	/		N	/		/	/	/	/	■	20	
Dec.......	N	/	/	/		/	/	/			/		/	/		/		N	/		/								/			13	
Jan.......																																0	
Feb.......																					/		/	/		/	/	/		■	■	6	39
Mar.......	/	/	/		/	/	/	/	/		N	/	/		/	N	/		N	/	/		N	/	/	N	/		/		/	19	
Apr.......	/			/	/	/	/		/	/		/		/	/	/	/	/		N	/		/	/	/	/		/	/	/	■	21	

FIG. 12. (*Concluded.*)

ever, have an irregular rhythm. While the observed rhythm is rarely entirely regular, yet each hen tends to produce eggs according to a rhythm that is characteristic to a certain limited degree for that individual. Superimposed on the daily rhythm are evidences of other rhythms having a beat measured by months or years. Although from another standpoint egg production is a more or less continuous process, at least in so far as the growth of the yolk is concerned, even though the fluctuations in the activity of the albumen and shell glands may be more pronounced, the rhythm may be considered as it appears on the record sheets, *i. e.*, the rhythm shown in the deposition of the eggs. Various types of rhythm have been observed. If, as a working basis, it be assumed that an egg a day represents a standard rhythm, although this high rhythm is rarely reached for extended periods, it will be found that some hens lay every other day, or we may say a one half rhythm, others two thirds, *i. e.*, two days out of three, others three fourths and so on. The three fourths or four fifths rhythm is common among most good layers. Occasionally the series may be repeated without the intervention of a zero day as is shown by the time of day the eggs are laid, for if the time of day at which the eggs are collected from the trapnests is recorded, the rhythm is shown even better than by the daily records. It has been our practise to visit the nests about every hour and a half and to record the time the eggs were gathered in units of a half hour. Thus the approximate time that each hen drops her egg is known. Rhythm, as shown by the time of day a hen lays her eggs, is an index of the essential continuity of the activities of the ovary in the growth of the ova, rather than of any rhythm in its activity, since the interval between eggs is more uniform than when the daily record only is used. One may perhaps infer that there is some rhythm in the activities of the oviduct since it is known that the stimuli for its activity comes from the presence of the yolk in its lumen. However this may

be, the several types of rhythm shown by the daily records are found to depend very much on the time of day that the eggs are laid.

None of the various types of rhythm, *i. e.*, one half, three fourths, etc., are characteristic of any one hen, although many individuals seem to center about a particular rhythm, *e. g.*, two thirds. A bird with this rhythm may fall to the one half type but does not often, except in the spring, exceed the three fourths type. While little stress can be laid on this point, it is interesting to note this tendency toward a definite rhythm in some individuals. But aside from these considerations, birds of the same age, which begin to lay at approximately the same time and which do not become broody, do not lay with the same rhythm. Thus, of two full sisters, hatched the same day, one laid only about every other day, while the second laid about five days out of six. The rhythm, then, is quite an important factor in determining the number of eggs laid.

Various causes may interfere with the normal rhythm, such as causes that interfere with the formation and growth of the egg, and other causes such as environment, season, method of management and internal factors such as broodiness. In many birds evidences of a rhythm with a period of some length may be noted as shown on page 215. The example given is of course idealized but actual records of nearly the same type may be observed.

In this connection the question of the nonproductive periods, usually of short duration, that occur in some records and which produce irregularities in the rhythm may be discussed. As will be pointed out later, broodiness is responsible for some of these periods. A similar period, that may be noted in some hens' records during the winter, may be taken as an index of the existence of a winter cycle. But other individuals may have two or more such periods or may have a single period fairly early in the winter (No. 4529, Fig. 13). Some of these periods may be inherent in the individual's makeup but

No. 4529 HATCHED MARCH 7, 1915. AGE AT FIRST EGG, 214 DAYS

Date 1915–16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Sept.																															■	0	
Oct.							7.5	7.5	9	9	10.5	9	9	9	9.5	1		7.5	7.5	7.5	9	4.5		10.5								16	
Nov.																															■	0	
Dec.																						N4										0	
Jan.											N3	10.5		8	9	9	11	1				9	3		7.5	10.5	3	N 11.5	9	10.5	3	14	
Feb.		7.5	10.5	3		7.5	10.5	3			10.5	11.5	2		7.5	9	9	10.5	10.5	3			9	10.5	7.5	9	10.5	9	10.5	■	■	22	52
Mar.	10			N 10.5	N4		N1		N1		N9					N9	N3		N 9.5	N3		N9	N9	N 11.5	N3	N 12	N3		N9	9	11	3	
Apr.	3		7.5	N11	11	1	N3		N 7.5	N1	N9	N9	N9	9	N3	9	10.5	N 10.5	3		7.5	9	10.5	10.5	9	10.5	9	10.5	10.5	N 3	■	17	

No. 5032 HATCHED MARCH 28, 1915. AGE AT FIRST EGG —

Date 1915–16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Nov.																											N4	N 7.5	N1		■	0	
Dec.	N 10.5	N 2.5		N 9	N 3		N 10.5	N 1	N 4		N 9	N 3		N 1	N 2.5		N 1	N 3		N 1		N 3		N 3		N 3						0	
Jan.																							N 12	N 1	N 3		N 7.5	N 10.5	N 1	N 4.5		0	
Feb.	N 9.5																									N 7.5	N 12	N 1	N 1	■	■	0	0
Mar.	N 1	N 4		N 3		N 3		N 7.5	N 10.5	N 1	N 4		N 9	N 10.5	N 1	N 4		N 9	N 3	N 3		N 10.5	N 3	N 3		N 9	N 10.5	N 1	N 4		N 9	0	
Apr.	N 10.5	N 12	N 3		N 9	N 10.5	N 1	N 4		N 9	N 10.5	N 10.5	N 3		N 7.5	N 10.5	N 10.5	N 10.5	N 3		N 7.5	N 9	N 10.5	N 3	N 4	N 7.5	N 9	N 10.5	N 3	N 3	■	0	

FIG. 13. Types of Records. No. 4529 is that of an early maturing pullet that laid discontinuously but nevertheless made a fairly good winter record. Nos. 5032 and 246 are nesters, *i. e.*, birds that visit the nests regularly but do not lay. The time at which the egg was collected or the hen ready to leave the nest is shown by the numerals. ".5" is used for the half-hour period.

HATCHED MARCH 30, 1913. AGE AT FIRST EGG —

Date 1913–14	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Nov.																															■	0	
Dec.																																0	
Jan.														N 3		N 11.5		N 9.5	N 3		N 9.5	N 1		N 11.5	N 3.5		N 1.5		N 11	N 3		0	
Feb.	N 1		N 1		N 11.5		N 1.5		N 9	N 3																		N 4	■	■	■	0	0
Mar.				N 11.5 N2			N 8	N 11.5	N 3.5		N 10.5	N 2		N 10	N 1	N 2		N 9	N 1.5	N 4.5		N 9.5	N 11.5	N 2.5		N 9	N 10.5	N 3.5		N 8.5	N 10.5	0	
Apr.	N 2		N 10.5	N 10.5 N2.5	N 3.5		N 10.5	N 11.5	N2 N 3.5		N 10.5	N 10.5	N 2		N 8.5	N 11	N 2		N 7.5	N 10	N 11.5	N 11	N 2	N 2		N 7.5	N 10	N 11	N 2	N 2.5 N4	■	0	
May		N 8.5	N 10	N 10	N 2	N 2		N 8.5			N 2		N 8.5	N 10	N 11.5 N2	N1 N3		N 8.5	N 10	N 11.5	N 11.5	N 3.5		N 9.5	N 10	N 2	N 2		N 8	N 11.5	N 2	0	
June		N 8	N 10	N 11.5	N 1.5		N 10	N 10	N 10	N 11.5	N 1.5		N 1.5		N 2		N 8.5	N 10.5	N 2		N 10	N 11.5	N 2	N 8.5	N8 N 10	N 11.5	N 1.5		N 8	N 10	■	0	
July	N 10.5	N 11.5	N 2	N 3		N 8.5	N 10.5	N 2																		N 7.5		N 11 N2		N 1.5		0	
Aug.	N 8.5	N 12 N 2.5		N 11	N 4		N 8.5	N 11	N 2.5		N 8.5	N 10	N 4		N 8.5	N 12	N 2	N 8.5	N 11	N 10.5	N 1.5	N 4		N 8.5	N 11	N 1.5		N 10	N 11.5	N 3.5		0	
Sept.	N 9	N 11.5	N 3.5		N 10	N 1.5		N 10	N 2.5	N 4		N 8.5	N 12	N 3		N 10	N 4		N 8.5 N 11.5	N 1	N 3.5		N 9.5	N 1.5		N 11.5	N 4		N 10.5	N 1.5	■	0	
Oct.		N. 11			N 11.5 N1		N 11.5		N 1.5																							0	

FIG. 13. (*Concluded.*)

Years' Total 0

others are probably the result of the environment, since it is well known that nonproductive periods can be induced by artificial means.

One of the most interesting things in connection with the rhythm of egg production as observed by Pearl ('12) is the existence of hens which never lay an egg, but the record of whose visits to the nests shows a very definite rhythm. A number of such hens have appeared in our flocks. (Nos. 5032 and 246, Fig. 13.) The hour of their visits to the nest exhibits exactly the same sort of rhythm as normal hens. These facts point strongly to the existence of some mechanism other than the formation and deposition of an egg which controls the extrusion of the egg. It is interesting to note that if one of these hens is removed from the nest before she is ready to leave, she returns and persists in doing so until, shall we say, she thinks she has laid her egg. Autopsies of several of these hens show that they fall into two classes; viz., those that are producing yolks or eggs but depositing them in the abdominal cavity, and those in which a tumor of the reproductive system is involved.

Laying hens often visit the nest at the proper day and hour but fail to lay. Such hens (No. 4529, Fig. 13) usually lay the day previous and the day after in regular routine, though at times they may pay two or more such nonproductive visits in succession.

A study of these latter records shows that some hens have indications of a potential capacity greater than the actual capacity revealed in the records. Very many hens pay an occasional visit to the trap nest without laying (note the *n*'s in the various records), while a few pay such visits more or less regularly, at various periods of their lives. The striking feature of these visits is that they are made at the hours one would expect if an egg were actually laid (No. 4529, Fig. 13), though the nature of the stimulus that causes such visits is uncertain.

Broodiness.—Broodiness, from the commercial as well as biological standpoint, is one of the most important of

the factors influencing egg production. In general, with the onset of the first broody period, the monthly production falls off 40 per cent. of its former rate. Broodiness, however, as met with in the laying hen, is to some extent an artificial condition. In a free state a hen becomes broody after she has laid a clutch of eggs, incubates them, and rears a brood of chickens. Altogether she is not producing eggs for a period of some ten weeks or more. After this she may again lay a clutch and repeat the process. Egg production under such conditions remains at a relatively low ebb. It is a matter of common knowledge among poultry keepers, however, that by various means the broody hen can be "broken up." That is, she can be induced to discontinue manifestations of broodiness and after a period varying from a few days to several weeks will begin to lay again. As a rule, however, only a few—ten or twelve—eggs are laid before a hen goes broody again. The process may be repeated indefinitely.

There is a considerable variation in the number of times a hen goes broody in a year, the length of the broody periods, the trouble required to break her up and other characteristics of broodiness.

The age at which the first broody period occurs depends in part upon the time a hen begins to lay. In the vast majority of instances egg production precedes broodiness. At least 15 to 20 eggs are laid before a hen becomes broody, though it may be many times that number. *Age incidence* in the first place depends upon the age at which the hen lays her first egg but after that it depends upon other circumstances, which have not been determined. Thus, the age of a bird at her first broody period may vary from eight months up to the end of the second year. Usually, however, the first broody period comes on when the bird is from 11 to 15 months of age. After the first broody period, the periods recur about once a month, if the hen is promptly broken up. There are records in our files of a few Rhode Island Red hens

that have not been broody for from one to three laying years.[5]

The number of broody periods per year, then, depends upon the date of the first period and in the second place upon the cessation of production in the fall. Egg production usually, but not always, ceases with a broody period.

A broody period has two phases. First, the period of manifestations of broodiness such as clucking, ruffling of feathers and cessation of production. This period is variable, some hens being easy to "break up" while others are very difficult. Manifestations of broodiness sometimes begin several days before egg production ceases, and may rarely continue without cessation of egg production or without hanging to the nest. I do not recall a case when egg production began before the cessation of the manifestations of broodiness.

The second phase begins with the disappearance of the manifestations of broodiness, and extends up to the time egg laying recommences. Its chief characteristic is non-productiveness and its length varies considerably.

Broody periods coming during the height of production, March and April, are usually of short duration, but gradually lengthen as the summer advances, until they sometimes last for a month or more. During the winter months, the periods are longer than those occurring during the spring and often lead to the cessation of egg production for several months.

Egg production is affected by broodiness chiefly through the number of broody periods. Hens that go broody many times during the year have a much lower production than others that go broody only two or three times, other things being equal. It is of particular interest to note the abrupt way in which the monthly egg production usually decreases with the onset of broodiness, regardless of the time of the year. Thus, a hen

[5] The statements in this section are based on an intensive study of broodiness, the data on which will be published in due course of time.

may be laying at a 75 per cent. rate before going broody, but with the appearance of the first broody period production falls off 40 per cent. of its former rate. In general it has been found that for each hen the rate for the broody part of the year is only about 60 per cent. of the rate of the nonbroody part.

It is not known whether the intense development of broodiness in the summer months is directly due to the weather conditions as such or whether it is due to some internal cause or is part of the annual cycle. At any rate it is evident that it operates to decrease the egg production very considerably. Further discussion will be postponed until the study of broodiness now in progress is ready for publication.

Types of Winter Records.—The various factors described in the foregoing pages combine in many ways and produce as a result different types of records, several of which may now be discussed in more detail. For the present we may divide the various types of records into high (over 30 eggs), mediocre (under 30 eggs) and zero producers.

High producers (over 30 eggs) may be divided into several subclasses. First, the early maturing, nonbroody high that lays continuously at a high rate and makes a very high record (No. 4846, Fig. 3). Second, the late maturing nonbroody high that lays continuously at a high rate but makes a lower record than the first in direct proportion to the difference in maturity. (See Figs. 3 and 4.) Third, the broody, early maturing high that lays at a high or fairly high rate during the laying periods (not shown). Such a bird's record is cut very materially by the broody periods. Individuals of this type are not very numerous during the winter period. Fourth, there is the high bird that exhibits a pronounced winter cycle or period of good production during the early part of the winter, but which stops after a time and may not lay at all for several weeks. This type is closely related to the bird that lays her eggs in clutches, but because of her

early start makes a comparatively high record. Finally there is the type of bird shown by No. 4797, Fig. 11, that matures early, lays steadily and does not go broody but lays at a comparatively slow rate. Such birds may make high records, but they never make the highest ones.

Mediocre producers (under thirty eggs) may result from any one of the various types previously described for high producers through the failure of one or more factors. Thus, delayed maturity will cause a bird to fall below the dividing line at 30 eggs to a degree that will vary inversely with the age at first egg, due allowances being made for the date at which the individual was hatched (Fig. 4). Or a bird may fall below the required number of eggs through a slow rate of production (No. 5080, Fig. 11, or Nos. 224 or 284, Fig. 12). The former type of bird (Fig. 4) would seem to be a late maturing high, since it is clear that its record results directly from the variability in time of first egg. Hence this type of mediocre producer is to be regarded as an artificial class rather than a real class as in the case of the birds typified by No. 5080.

Zero producers, by definition, are birds that do not lay until after March 1, and need no further discussion, except to note that some of them clearly result from the combined effects of date of hatch and age at first egg rather than from an inherent inability to lay during the winter (*i. e.,* from a lack of the winter cycle).

There are, then, numerous types of records resulting from the interaction of the various components described in the earlier part of the paper. Although the records described are winter records, the observations apply equally to annual egg production. High egg production results only from a combination of the right set of factors. If any one of several of these factors fail, egg production is lowered.

(To be concluded.)

BACTERIAL PHYLOGENY AS INDICATED BY MODERN TYPES[1]

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The importance of the group we call bacteria in any theories concerning the origin and evolution of life on our planet is well shown by several recent writers on the subject, notably Jensen (1909), Osborn (1916), and Kligler (1917). In each case, however, there are certain misinterpretations of our knowledge of the modern bacteria and their function which go far to invalidate, or at least to weaken, the specific conclusions which they reach with reference to the types of primitive bacteria.

In our search for hints as to ancestral types by investigation of modern species of bacteria we must hold in mind that although present-day bacteria approach most closely to what we conceive must have been primitive life, nevertheless and for this very reason the group of modern bacteria must have the longest evolutionary history of any existing group. That any modern species closely resembles the original type is therefore not extremely probable. It can not be too often emphasized that in speculations concerning evolutionary history based upon modern forms with no adequate fossil ancestral types we must deal only with the tips of the ultimate twigs of the branches of the evolutionary tree. By a careful comparison of the surviving forms we may gain a knowledge of their probable relationships, but it should be remembered that in no case this relationship is that of parents and offspring, but that of brothers and cousins. Perhaps we may speculate upon the probable arrangement of the branches of the evolutionary tree that have disappeared

[1] From the Bacteriological Laboratories.

in past geologic ages by study of the survivors, but it is self-evident that there should be a perfect knowledge of these survivors, morphological and physiological, so that we may not be led astray by superficial resemblances when there exist, in fact, deep-seated and fundamental distinctions.

The geologic evidence that has been adduced as to the character of the primitive bacteria is of but the slightest value. Speculation as to the primitiveness of nitrogen fixers, for example, based upon the geologic evidence introduced is scarcely convincing.

It should also be noted that it is quite possible that the bacteria do not constitute an homogeneous group in the sense that all are descended from a single primitive type of bacterium. It may be that there have been included in the group bacteria forms which have assumed similar morphological or physiological characters without having a common ancestry. Botanists, for example, at the present day are by no means convinced that seed plants have all had a common origin; in other words, the ability to produce seeds may have arisen independently in two or more groups of the fern plants. It is possible that some of the forms we term bacteria have been derived from the fungi, others from the blue-green algæ or possibly some even from the protozoa. In short, it may be that the actual relationships existing between various bacteria may be very distant.

A study of these modern bacteria will reveal relationships such as those just indicated. The possibility that the bacteria are a derived group must be constantly held in mind. To prove that they are primitive it must be shown that no group from which they might have sprung or to which they seem to be related can be regarded as more primitive. This has not been satisfactorily accomplished in certain cases.

Modern systematic bacteriologists are in fair agreement that there should be recognized five or six distinct groups or orders of bacteria. Of these, the *Eubacteriales*,

or true bacteria, are generally regarded as the least specialized and possibly the most primitive. It is possible that the great group of the sulphur bacteria, the order *Thiobacteriales,* is equally primitive, though the genera and species have been less studied and are not as well known. There are unquestionably many intergrading forms between the *Eubacteriales* and the *Thiobacteriales,* as shown by close parallel series of morphological types. It seems equally clear that there are intergrading forms between the *Thiobacteriales* and the blue-green algæ. Morphologically, too, one may find every gradation between the typical colorless, sulphur-containing *Beggiatoa,* through species of this genus showing bacteriopurpurin, through the faintly colored, slender *Oscillatoria* to the thick, deeply pigmented forms. If these intergradations and indicated relationships are real, it is apparent that the true bacteria may have come from the blue-green algæ through the sulphur forms, or the blue-greens may have come from the true bacteria, or the sulphur forms may be closer than either of the other groups to the primitive types from which all three groups have been derived. While there is no definite proof apparently possible at the present time, it is not at all improbable that the last assumption is the true one. A relationship quite certainly exists between the group of sheathed filamentous bacteria (the *Chlamydobacteriales*) and the blue-green algæ. The resemblance is so well marked that certain species of the iron bacteria are quite commonly included by algologists among the algæ. The relationship to the *Eubacteriales* is not quite so clear. Possibly the genus *Sphærotilus* (*Cladothrix*) may be regarded as a link, for this organism consists of rod-shaped cells occurring in chains, all embedded in a gelatinous sheath. Motile cells (gonidia) with polar flagella somewhat resembling *Pseudomonas* types may be developed.

The fungi apparently are related to certain of the bacteria through the *Actinomycetales.* This latter group has some resemblance to certain of the true bacteria such

as the *Lactobacillus* of sour milk and the diphtheria types. It is possible that these organisms together with a few genera from the *Eubacteriales* represent an entirely distinct series. The *Spirochætales* apparently constitute a group showing combinations of characters which relate them to the *Eubacteriales* and the *Thiobacteriales* on the one hand, and the *Protozoa* on the other. The group *Myxobacteriales* is apparently related to the true bacteria, but not to higher groups of plants or animals, unless there may be some as yet undiscovered relationship between these forms and the slime molds as suggested by a superficial study of their fruiting forms.

The interrelationships just discussed among the various great groups of bacteria may be illustrated by the following diagram in which the connecting lines are intended to show relationship, but not necessarily derivation.

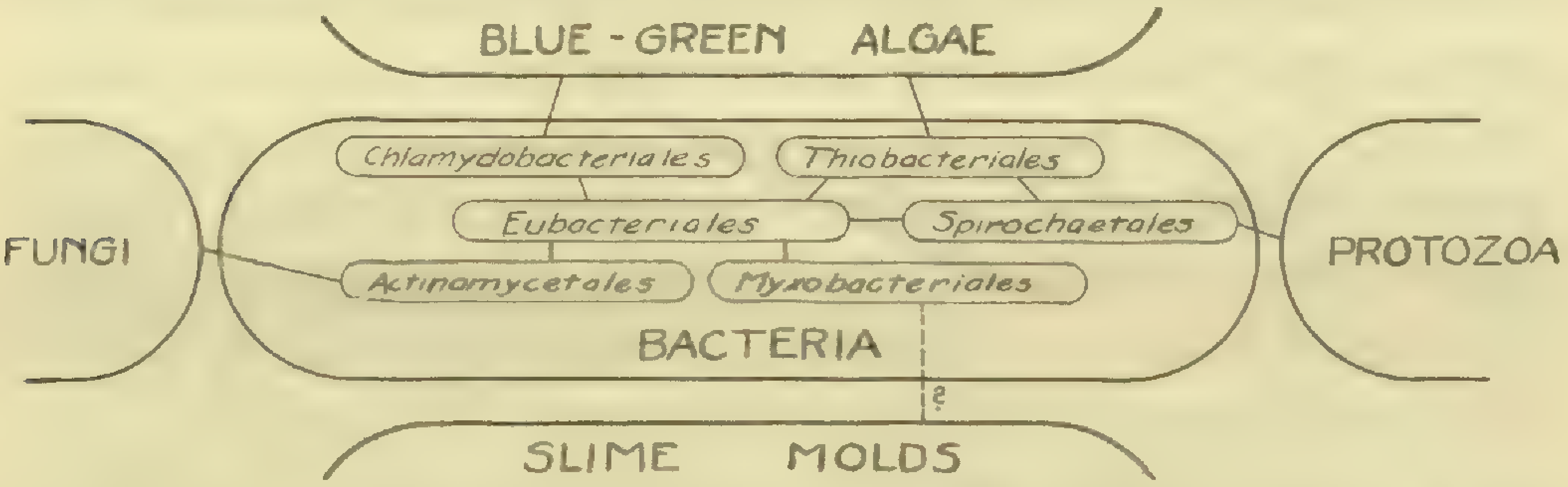

FIG. 1. CHART ILLUSTRATING THE PROBABLE INTERRELATIONSHIPS OF THE GREAT GROUPS OF BACTERIA AND THEIR RELATIONSHIPS TO OTHER GROUPS, as Fungi, Blue-green Algae and Protozoa.

From the standpoint of the student of evolution the order *Eubacteriales* (possibly also *Thiobacteriales*) is of special interest, for within it is probably to be found greater variation in physiological activity than in any other group of plants or animals. A comparison of the modern forms belonging to this group may well give some hint as to their evolution. Too much can not be expected, however, without getting far into the realms of speculation.

After rather careful consideration a committee of the Society of American Bacteriologists has proposed a list

of names to be recognized as valid for the genera of this order. They have also suggested that these genera be grouped in seven families. Altogether twenty-eight genera are recognized. It should be possible, if adequate knowledge is at hand, and the *Eubacteriales* constitute an homogeneous group, so to arrange these genera as to show their probable and their possible relationships, and perhaps gain some knowledge thereby of their origin and evolution.

From the standpoint of the evolution of bacteria we are much interested in the organisms which can live and grow in the total absence of organic matter, those which utilize inorganic substances exclusively in the manufacture of their own food, in short, those bacteria which are strictly prototrophic.

Let us consider the possible sources of the various elements needed in the building up of the primitive bacterial protoplasm. We have no reason to suppose that such primitive bacterial protoplasm differed in any marked degree from the protoplasm of modern forms. Such organisms must have available carbon, hydrogen, nitrogen, oxygen, sulphur, phosphorus and iron, with small quantities of a few other elements. Upon the earth before the advent of other plant life, the carbon necessary for growth would probably be secured from carbon dioxide, or possibly from methane or carbon monoxide; the hydrogen was undoubtedly present in abundance in water, perhaps traces also of the free element, of methane, or of ammonia may have been available; the nitrogen was probably present in sufficient quantities either as ammonia or as nitrates, and of course in the form of less available, relatively inert, gaseous nitrogen; the sulfur probably existed as sulfids, sulfates, and free sulfur; the phosphorus was probably found in phosphates and the iron in both ferrous and ferric condition. It is evident that elements and compounds were present in abundance and variety, but not in the form of *organic* compounds. All modern living organisms are divided into those which

require their food to be ready manufactured for their use, and those which can manufacture their own food (prototrophic). It is apparent that the primitive organism was probably prototrophic.

The manufacture of food from inorganic materials requires the expenditure of energy. We must account, if possible, for the sources of such energy for the prototrophic forms. Among modern organisms the energy needed is secured always from one of the two sources, light rays or chemical oxidation. While other types of energy are known, apparently plants have not been adapted to their utilization. If light rays were first used as an energy source, the primitive organism was probably provided with some pigment which was of significance in the absorption of the light and in its conversion into chemical energy. Among modern forms which may have resembled such primitive organism may be cited the simpler types of the blue-green algæ and the phototactic sulphur bacteria containing the pigment bacteriopurpurin. If the Chamberlin planetesimal hypothesis of earth origin is accepted, such might very possibly have been the primitive types. However, primitive conditions may have been such that light energy was not available. Organisms developing under such conditions must have been directly dependent upon chemical energy. Such energy might be secured by the oxidation of ferrous iron, of free sulphur or of the sulfids (particularly hydrogen sulfid), methane, hydrogen, carbon monoxid and ammonia. Organisms among modern species are known which can utilize each of these methods of securing energy. There is no reason, therefore, why any one of these should not be a method used by a primitive form. The modern types of organisms which oxidize ferrous to ferric iron are in many respects among the most highly differentiated of the filamentous bacteria and show many points of resemblance to the blue-green algæ. They show few primitive characters, and are probably to be regarded as not closely related to the primitive bacteria.

A study of the organisms which at the present time are known to secure energy by the oxidation of H_2S, CH_4, H_2, CO and NH_3 show that they possess certain characteristics in common. For the most part the organisms are cocci or rods, occasionally spiral, in some cases motile, and then always with polar flagella. While there are some exceptions to the rule, the organisms for the most part do not thrive in a medium containing much organic matter. It is not improbable that the primitive organism had characters not greatly unlike these enumerated. Just what type of oxidation is most primitive it is difficult if not impossible to determine, although certain conjectures may not be out of place. Probably one of the most common of the easily oxidized substances of the primitive earth was hydrogen sulfid. It undoubtedly was a common constituent of thermal springs. The modern representatives of the groups which thrive in water containing hydrogen sulfid are abundant both in numbers and in species. By means of the energy which they secure from the oxidation of H_2S and S they probably take up CO_2 and transform it into food and protoplasm. Apparently all of the forms which have been investigated are motionless cocci or rods or spirals motile by means of *polar* flagella. No modern form is known which produces spores. Many of the species contain a pigment bacteriopurpurin and swim or grow toward light, showing positive chemotaxis or chemotropism. We may find every gradation between the modern representatives of these forms and the blue-green algæ, on the one hand, and the true bacteria, on the other. Many of the blue-green algæ contain a purple coloring material in addition to the blue and green pigments. From the standpoint of evolutionary requirements, therefore, it is evident that some primitive organism having much the same type of metabolism as the modern sulphur bacteria would be a satisfactory starting form.

Before additional stress is laid upon a sulfur bacterium as a possible progenitor of modern forms, we

should examine carefully other possibilities. It is conceivable (though scarcely probable) that hydrogen may have constituted a larger percentage of the atmosphere in times past than now. Several species of modern bacteria have been described which in the presence of hydrogen and oxygen may secure their growth energy by combining these elements directly or indirectly. These species are motile rods with *polar* flagella. These modern members of the genus *Hydrogenomonas*, however, are very far from primitive because under ordinary conditions they are pantotrophous growing well on ordinary laboratory media. Thus far no organism strictly prototrophic capable of utilizing hydrogen has been found. This does not prove that such organism has not existed, but throws the burden of proof upon any one who would urge hydrogen oxidation as a primitive method of securing growth energy. The results of Kaserer (1906) seem to indicate that the organism catalytically causes the transformation in the presence of hydrogen of carbonic acid into formaldehyde, the cell then using the formaldehyde as food.

Methane and carbon monoxide are also oxidized by certain of our modern bacteria, the organisms securing their growth energy in this manner. These organisms according to the descriptions are autotrophic and do not thrive in the presence of organic material. It is possible that these represent primitive characters. The organisms are rods, motile or non-motile, when motile with *polar* flagella. If either methane or carbon monoxide were common in the atmosphere of the early earth, forms of this general type may have flourished. That these gases were sufficintly abundant does not seem probable, but the possibility must be admitted.

Several types of modern bacteria are known which oxidize ammonia to nitrites and nitrites to nitrates, utilizing the energy thus secured for chemosynthesis of food from inorganic materials. At least one species of the nitrifying bacteria is a coccus, others are rods, motile by

means of polar flagella. It is not at all improbable that ammonia may have been abundant enough on the primitive earth to have constituted an adequate energy source for the primitive bacteria.

Which of these modern types most closely resembles the primitive organism living on autotrophic existence? It is perhaps impossible to say. The modern representatives of the nitrifiers and the methane and carbon monoxid oxidizers are apparently rather isolated groups without numerous species and apparently not closely related to other forms. The sulfur oxidizers, on the other hand, are abundant, of many types, and show many intergradations with other bacteria and the blue-green algæ. Possibly a somewhat better case can be made out for them. However, it should be noted that all of these forms have certain characters in common, they are all autotrophic, all are aerobic, and when motile are elongate cells with polar flagella. It is perhaps a fair inference that the aerobiosis and the polar flagellation are primitive characters. We may well conclude with Jensen that all of these organisms discussed are related and may be

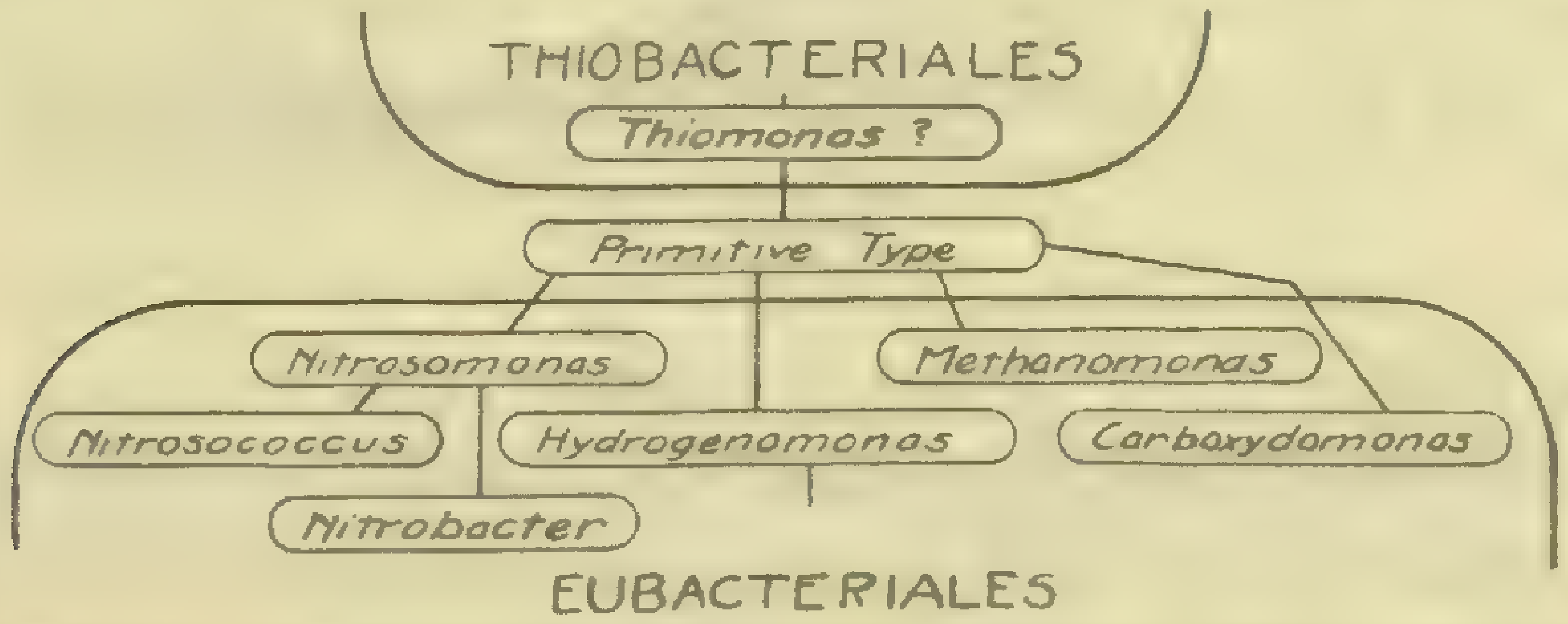

Fig. 2. Probable Relationship of certain modern Genera of Bacteria to the Primitive Organism and their Relationships to each other.

placed in a single group. Expressed in terms of modern representatives of the primitive types, the following diagram might express the idea.

We may next concern ourselves with possible and probable relationship of these various forms to other members of the *Eubacteriales,* disregarding the *Thiobacteriales.* The remainder of the *Eubacteriales* differ from the autotrophic forms thus far discussed in that in

every case they require the presence of organic carbon compounds in the substrate in which they grow. These compounds may be of the greatest diversity of types, but none of the bacteria are capable of manufacturing their own carbon food. It is possible that other types of bacteria than the prototrophic may not have developed upon the earth until after the evolution of higher plants, such as the algæ, upon which they could depend for food. Possibly there may have been some start made, however, in the utilization by one type of organism of the dead bacterial protoplasm of another type.

How may we detect relationships of modern metatrophic bacteria to these more primitive types? Possibly by a study of intergrading forms. The genus *Hydrogenomonas* apparently is either autotrophic or metatrophic according to the conditions of the environment. Some primitive organism may have acquired properties similar to those of the modern *Hydrogenomonas* and constituted the progenitors of the modern forms. Possibly this type of differentiation may have arisen in several groups. It is conceivable, for example, that some organism having characters such as *Nitrosococcus* might have given rise to an independent branch, possibly to forms like *Micrococcus*. This, of course, is pure speculation.

Among the metatrophic bacteria we are probably justified in placing the genus *Pseudomonas* as most closely related to the forms discussed because of its close morphologic resemblance, with rod-shaped cell and polar flagella, to the autotrophic forms; then too, there is the evidence of the intergrading *Hydrogenomonas*. Somewhat less diversified in nitrogen metabolism are the related genera *Azotabacter* and *Rhizobium*, both usually with polar flagella. rod-shaped bodies, primitive nitrogen requirements, and marked capacity to utilize carbohydrates, oxidizing them quite completely to CO_2 and H_2O. The supply of energy is so abundant to these organisms that in the absence of sufficient combined nitrogen in the substrate they can fix atmospheric nitrogen, and build it into their protoplasm.

This nitrogen fixation must be carefully differentiated from the nitrification previously discussed. Probably the non-motile group *Mycoderma* which resembles the other organisms in ability to oxidize sugars (preferably ethyl alcohol), but is non-motile, should be placed here. These three genera are obligate aerobes and secure their growth energy by relatively complete oxidation of carbohydrates, alcohol or even acetic acid. They apparently constitute a natural group related to *Pseudomonas.* It should be recalled that a statement of relationship does not imply derivation, but simply common ancestry.

We have now considered all the bacteria which show the primitive characters of polar flagellation and obligate aerobic utilization of carbonaceous foods. In the genus *Pseudomonas* we find evidences of differentiation in metabolism, particularly ability to bring about proteolysis. In some species we have evidences of adaptation to anaerobic conditions, among the so-called denitrifiers. Some members of this group are capable of taking oxygen from nitrite and nitrates under anaerobic conditions, with evolution of free nitrogen. Other forms are known that can reduce sulfates to sulfids. Such facultative anaerobes, securing oxygen from an easily reduced compound, evidently make use of the oxygen in the same manner as though growing under aerobic conditions for the oxidation of carbon compounds. The next step in the development of anaerobiosis was probably the utilization of carbon compounds, securing growth energy by intramolecular oxidations; in such forms fermentative capacity becomes well marked.

The close relationship in morphology and physiology existing between the short spiral *Vibrio* and *Pseudomonas* indicates that the family *Spirillaceæ* has come from an ancestry having much in common with *Pseudomonas.*

The other bacteria belonging to the *Eubacteriales* are more specialized in general morphology and in physiology than the forms thus far mentioned. When motile the cells are peritrichous rather than with polar flagella.

Some forms have developed the ability to produce endospores (family *Bacillaceæ*) and seem to comprise a closely related group of genera whose relationship to the more primitive types is somewhat problematic. Another well-marked group of bacteria includes the large series of (usually) gram-negative bacteria that produce no spores. These may be included in a family *Bacteriaceæ*. With the exception of polar flagella, there is no very marked difference between the *Pseudomonas* forms and the *Proteus* types. It is quite possible that they are closely related. The cocci apparently form another homogeneous group, the *Coccaceæ*. The affinities of the group may be sought in several places. For example, there is apparently very close resemblance culturally and physiologically between the chromogenic cocci and the chromogenic rods closely related to the genus *Bacterium*; the organism usually termed *Bacillus prodigiosus* (*Serratia marcescens*) is remarkably near certain red cocci as *Rhodococcus roseus*. The possibility that there is a relationship between the *Nitrosococcus* and *Micrococcus* has already been pointed out. Then there is a decided relationship evident between the aciduric bacilli and the genus *Streptococcus*. All of these origins are possible; if all these relationships are true, the group *Coccaceæ* must be regarded as heterogeneous, that is, polyphyletic.

The group containing the tubercle bacillus (*Mycobacterium*) and diphtheria bacillus (*Corynebacterium*) shows undoubted relationships to the order *Actinomycetales*. If they have no common origin with other genera of the *Eubacteriales* they should be included in the order *Actinomycetales*. However, there is decided evidence of relationship through *Leptotrichia* and perhaps *Erysipelothrix* to the lactic acid bacteria. If this is a valid relationship it would indicate that the *Actinomycetales* are an offshoot of the *Eubacteriales*, or at least have a common ancestry.

The various relationships illustrating the probable phylogeny of the class Bacteria is illustrated in the ap-

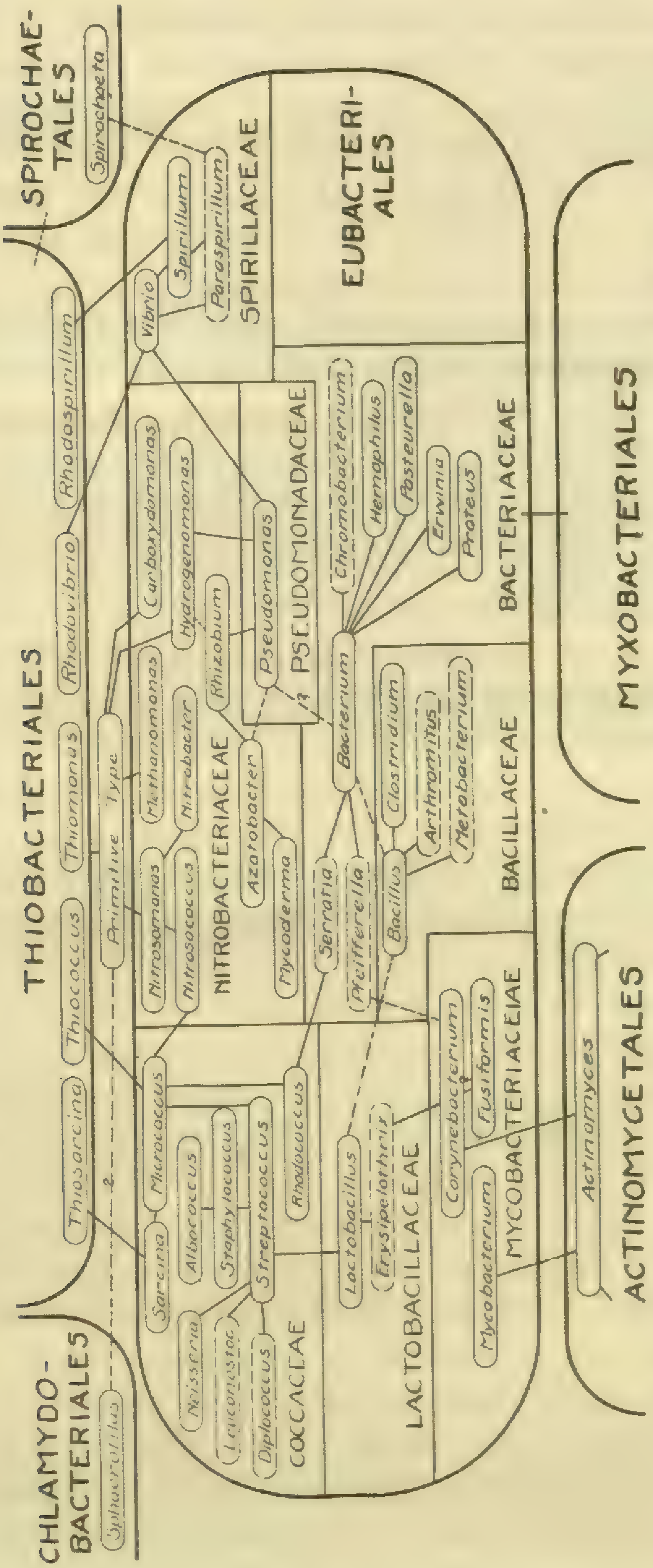

Fig. 3. Suggested Interrelationship of the Genera, Families and Orders of Bacteria.

pended diagram. Relationships which have appeared probable to the writer have been indicated by solid lines connecting genera, possible relationships have been indicated by dotted lines. The genera comprising the families recognized by the Committee on Nomenclature as belonging to a single family are enclosed by a heavy line. Genera not recognized by the committee are enclosed in dotted lines.

The foregoing analysis would seem to indicate that the grouping of genera by the Committee on Classification, with some slight modifications possibly, represents fairly well true phylogenetic relationships of the bacteria. The exact boundaries of the families are of course of little importance providing the scheme of classification tends to show relationships.

DISPROOF OF A CERTAIN TYPE OF THEORIES OF CROSSING OVER BETWEEN CHROMOSOMES[1]

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I

Two types of relations have been proposed to account for the facts of "crossing over" between pairs of characters that follow the same pair of chromosomes. One is a varying relation between the substances forming the factors belonging to *diverse pairs* in the same chromosome; the other a varying relation between the *two members of the same pair,* in the two paired chromosomes.

The former type is represented by the "chiasmatype" theory, held by Morgan and his associates, in which the diverse relations are held to be, or depend upon, the actual diverse distances apart of the factors extended along the linear chromosome. When the chromosome breaks, for any cause, it is more likely to separate two factors far apart than two close together; on this depends the varying cross-over ratios.

The second type is that brought to notice recently by Goldschmidt (1917), and commonly called the "variable force" theory. It is conceived that the two members of a given pair, as A and a, in the two paired chromosomes, may be held or drawn to their places by a pair of varying forces, which allow them to exchange places on the average in a certain proportion of cases; while B and b are held by a different pair of forces, which allows these two to interchange in a different proportion of cases; C and c by a still different pair, etc. The result would be diverse

[1] This paper arose and took shape during discussions on theories of crossing over in the Seminary on Genetics at the Johns Hopkins University.

ratios of crossing over when diverse pairs are compared; the cross-over ratio between A–a and B–b would be different from that between A–a and C–c, and so on. It is this theory that I propose to examine. I do not understand that Goldschmidt commits himself to any form of this theory, or to any theory that is exclusively of this type, so that this discussion is not presented as a commentary on his views, but on this type of theory for its own sake. Is it possible to explain the observed ratios of crossing over by any theory of this type?

To grasp the matter clearly, it will help to have an example before us. Let the following twelve groups of letters represent twelve pairs of chromosomes in twelve cells, each chromosome bearing two factors, which we will call A–B and a–b. The upper two letters in each pair show a single chromosome containing the factors A–B, the lower two the mated chromosome containing the factors a–b.

I.	AB	AB	A*B*	*A*B	AB	A*B*	AB	*A*B	A*B*	AB	AB	*AB*
	ab	ab	a*b*	*a*b	ab	a*b*	ab	*a*b	a*b*	ab	ab	*ab*

Now suppose that the forces holding A and a to their chromosomes are such that A and a exchange in one fourth of all cases, while B and b exchange in one third of all cases. That is, A and a exchange places in every fourth chromosome pair, B and b exchange places in every third pair. The letters that are thus to exchange with their mates are italicized in the pairs indicated above. The exchanges will evidently give the following result:

II.	AB	AB	Ab	aB	AB	Ab	AB	aB	Ab	AB	AB	ab
	ab	ab	aB	Ab	ab	aB	ab	Ab	aB	ab	ab	AB
			+	+		+		+	+			

By a cross-over is meant the fact that two factors of diverse pairs, as A and B, which in the germ cells that formed the parent were following the same chromosome (as in I, above), are found in the germ cells *from* those parents (II, above) to be following diverse chromosomes (as in the third pair of II, above); while conversely the two factors A and b, which were following diverse

chromosomes, are now following the same one. The cross-overs in II, above, are those indicated by the + sign; there are five of these. The ratio of the number of these new combinations (5) to the total number of germ cells (12) is the cross-over ratio; in this case the cross-over ratio is $5/12$, or .417.

Examination of this case will illustrate an important fact. *A cross-over is produced only when one of the two pairs exchanges while the other does not.* In the last pair to the right, in the example given above, the members of both pairs exchange places, but this does not give a cross-over—since A and B are still together, as they were before the double exchange.

Now if the number of exchanges for each pair of cells is different from that in the example given above, the resulting cross-over ratio will be different. By supposing each pair of factors, A–a, B–b, C–c, D–d, etc., to have its own characteristically diverse frequence of interchange of its members, all sorts of cross-over ratios could be obtained, varying from 0 to 1; that is, from no cross-overs to all cross-overs. The question in which we are interested is, could the observed cross-over ratios in such an organism as *Drosophila* be accounted for in this way?

It is to be noted that the problem as we take it up is independent of the nature of the forces that hold A and a (and the other factors) in their places, and that permit them to exchange in a certain proportion of cases. These forces may be utterly heterogeneous in the different cases; they may turn out to be of any kind whatever, so far as this examination goes. We ask merely whether, if the forces, whatever they are, give a constant average proportion of interchanges characteristic for each pair, they can yield the cross-over ratios actually observed.

II

It is evident that on this theory there are two kinds of ratios to be dealt with: the ratio of the number of interchanges of A and a (characteristic for each pair), and the ratio of the number of cross-overs, between two pairs A–a

and B–b; the latter of these ratios depends on the former. We shall call the former the exchange ratio; the latter is commonly known as the cross-over ratio, which we will designate by the letter C.

The exchange ratio signifies the ratio of the number of exchanges between A and a to the total number of germ cells:

$$\text{Exchange Ratio} = \frac{\text{Exchanges}}{\text{Total Number}}$$

The cross-over ratio (C) signifies, of course (following Morgan and the general usage), the ratio of the number of cross-overs to the total number of germ cells or progeny:

$$C = \frac{\text{Cross-overs}}{\text{Total Number}}$$

Goldschmidt (1917, page 90) has given a formula for the cross-over ratio resulting from any two exchange ratios, and has computed the resulting cross-over ratios from certain assumed exchange ratios. We shall give the formula a simpler expression than Goldschmidt has done; one that will enable us to determine its properties and limits of performance.

In cross-over ratios we deal with two pairs of characters, which we may designate A–a and B–b. Let x signify the exchange ratio for one of the pairs; and let y signify the exchange ratio for the other pair. Thus, if A and a interchange in one third of all cases, this pair's exchange ratio x will be one third (or .33⅓); while if B and b interchange in two fifths of all cases, its ratio, y, will be two fifths (or .4). For convenience we will always choose x and y in such a way that if there is any difference, x will designate the smaller ratio. That is, x will always be equal to or less than y.

Now, suppose that originally the first chromosome of the pairs bears the two factors A and B, the second a and b (as in I, above). After crossing over in the proportion

x, we shall have, in these first chromosomes of the pair, A and a in the following proportions:

$$\mathrm{x}a$$
$$(1-\mathrm{x})A$$

Similarly, in this same chromosome we shall find B and b distributed in the following proportions:

$$\mathrm{y}b$$
$$(1-\mathrm{y})B$$

(Thus, if A and a interchange in two fifths of all cases, then after interchange we shall, in the first chromosome, find a in two fifths of the cases, A in three fifths; and similarly for B.)

What will then be the proportions of the various combinations of the two pairs of factors? It will evidently be

$$\mathrm{x}a+(1-\mathrm{x})\mathrm{A}, \text{ multiplied by}$$
$$\underline{\mathrm{y}b+(1-\mathrm{y})\mathrm{B}}$$
$$=\mathrm{xy}ab+\mathrm{x}(1-\mathrm{y})aB+\mathrm{y}(1-\mathrm{x})Ab$$
$$+(1-\mathrm{x})(1-\mathrm{y})\mathrm{AB}$$

The cross-overs are aB and Ab, the proportion of which is evidently:

$$\mathrm{x}(1-\mathrm{y})+\mathrm{y}(1-\mathrm{x})=\mathrm{x}+\mathrm{y}-2\mathrm{xy}$$

The same result will be reached if we consider the second chromosome of each pair (that which originally contained a and b); so that the same proportion holds for both together. This, therefore, gives us our formula for the cross-over ratio in terms of the exchange ratios of the two pairs. It is essentially the same formula employed by Goldschmidt (1917), giving the same results, but written in more perspicuous form.

Let us therefore recapitulate in algebraic form the essential points.

Let

$$x = \text{exchange ratio of one pair,}$$

$$y = \text{exchange ratio of other pair}$$

$$(\text{so selected that } x \gtreqless y).$$

Then for the cross-over ratio (C) of the two pairs, the formula is

$$C = x + y - 2y.$$

An example or two will make the use of this formula clear. Suppose that the exchange ratio of pair A–a is $3/7$; of B–b it is $2/5$. Then

$$x = 2/5; \qquad y = 3/7$$

$$C = 2/5 + 3/7 - 2(2/5 . 3/7) = 17/35 = .486$$

Again, let

$$x = .31, \qquad y = .34$$

$$C = .31 + .34 - 2(.31 \times .34) = .439$$

(It is customary to express the results as percentages; thus the last example would give a cross-over ratio of 43.9 per cent. For our purposes it is more convenient to leave them as decimals.)

Now this formula has certain characteristics and limitations that allow us to bring the theory on which it is based to a test. The theory is that each pair has its characteristic exchange ratio; if that be the case, this formula holds.

We shall set forth certain of the important relations between cross-over ratio and exchange ratios, revealed by this formula; then show how these provide a test for the theory which the formula expresses. To aid in the comprehension of these relations, we give a table showing all cross-over ratios for two pairs of characters, resulting from the combinations of exchange ratios varying by tenths from 0 (no exchange) to 1 (all exchange). The table illustrates all the relations to be deduced from the formula.

Exchange Ratio for One Pair (A–a).

Exchange Ratio for the Other Pair (B–b).	0	.1	.2	.3	.4	.5	.6	.7	.8	.9	1.0
.0	0	.10	.20	.30	.40	.50	.60	.70	.80	.90	1.00
.1	.10	.18	.26	.34	.42	.50	.58	.66	.74	.82	.90
.2	.20	.26	.32	.38	.44	.50	.56	.62	.68	.74	.80
.3	.30	.34	.38	.42	.46	.50	.54	.58	.62	.66	.70
.4	.40	.42	.44	.46	.48	.50	.52	.54	.56	.58	.60
.5	.50	.50	.50	.50	.50	.50	.50	.50	.50	.50	.50
.6	.60	.58	.56	.54	.52	.50	.48	.46	.44	.42	.40
.7	.70	.66	.62	.58	.54	.50	.46	.42	.38	.34	.30
.8	.80	.74	.68	.62	.56	.50	.44	.38	.32	.26	.20
.9	.90	.82	.74	.66	.58	.50	.42	.34	.26	.18	.10
1.0	1.00	.90	.80	.70	.60	.50	.40	.30	.20	.10	0

Explanation of the Table

Table of the values of the cross-over ratios resulting from combinations of different exchange ratios, from 0 to 1, of two pairs of factors. Based on the formula:

$$C = x + y - 2xy$$

Where x = the exchange ratio of one pair,

y = the exchange ratio of the other,

and $x \gtreqless y$.

Outside the square (above and to the left) are the exchange ratios, by tenths, from 0 to 1; within are the cross-over ratios. To find the cross-over ratio resulting from any two exchange ratios, trace the rows and columns of figures from the two exchange ratios till they intersect; thus the cross-over ratio resulting from an exchange ratio in one pair of .6, in the other of .3, is .54.

The table shows directly the limiting values for the cross-over ratios from any two exchange ratios that are not exactly the same as those of the table. Thus:

If the upper left quadrant:

If x or y or both are below the values given in the table, the cross-over ratio is below the value given in the table. Thus if x is below .2 and y is below .3, the cross-over ratio is below .38. If both are below .10, the cross-over ratio is below .18.

If x or y or both are above the values given in the table, the cross-over value is above that given in the table.

In the lower right-hand quadrant:

If *x* or *y* or both are above the values in the table, the cross-over value is *below* that given in the table.

If x or y or both are below those in the table, the cross-over value is above that of the table.

In the other two quadrants (upper right and lower left):

If x is smaller and y larger than in the table, the cross-over ratio is above that of the table.

If x is larger and y smaller than in the table, the cross-over value is below that of the table.

Example: x and y given; limits of C required:

$x = .16, \quad y = .29; \quad C < .38$ and $> .26$

$x = .09, \quad y = .08; \quad C < .18$ and $> .0$

$x = .13, \quad y = .73; \quad C < .74$ and $> .62$

$x = .54, \quad y = .63; \quad C < .50$ and $> .48$

C given; limits of x and y required:

$C = .434$, x and y both $\leqq .434$, or both $\geqq .566$

$C = .021$, x and y both $\leqq .021$, or both $\geqq .979$

$C = .63; \quad x \leqq .37 : y \geqq .63$

$C = .96; \quad x \leqq .04 : y \geqq .96$

$C = .50; \quad x = .50 : y =$ any value from 0 to 1.

The formula for examination is:

$$C = x + y - 2xy$$

(in which x and y are proper fractions).

1. Two exchange ratios, x and y, give the same cross-over ratio (C) as do their complements, $1 - x$ and $1 - y$. For

$$x + y - 2xy = (1 - x) + (1 - y) - 2(1 - x)(1 - y),$$

as will be seen by performing the operations indicated in the second member of the equation. But this second member is the value of C for exchange ratios $1 - x$ and $1 - y$.

For example, the two exchange ratios .2 and .3 give the same cross-over ratio as do the two exchange ratios .8 and .7; for both cases $C = .38$. This relation is seen in the symmetrical constitution of the table; the cross-over ratio resulting from .1 and .2 is the same as that from .9 and .8; the cross-over ratio resulting from exchange ratios .4 and .7 is the same as that resulting from .6 and .3, etc. The rule holds equally for values not found in the table; thus the cross-over ratio resulting from .011

and .031 is the same as that resulting from .989 and .969.

2. If one of the two exchange ratios is changed to its complement, the cross-over ratio is changed to its complement.

That is, if the cross-over ratio resulting from x and y is C, the cross-over ratio resulting from x and $1-y$, or y and $1-x$ is $1-C$.

For:

$$x+(1-y)-2x(1-y)\equiv 1-(x+y-2xy)$$

But the first member of this equation is the cross-over ratio from x and $1-y$, while the second member is 1 minus the cross-over ratio from x and y. The same result is reached if we take y and $1-x$.

Thus, as the table shows, the cross-over ratio resulting from .2 and .3 is .38, so that the cross-over ratio from .2 and .7 is .62, as is likewise the cross-over ratio from .8 and .3 ($.38+.62=1$). Similarly, the cross-over ratio of .011 and .031 is .0413; hence the cross-over ratio from .011 and .969 is .9587.

3. When the cross-over ratio is less than ½, the exchange ratios x and y are either both greater than ½ or both less than ½; one can not be less than ½, the other greater. That is:

If $C<½$ then either $x<½$ and $y<½$ or $x>½$ and $y>½$. For let us suppose that $x=½-a$ and $y=½+b$, in which *a* and *b* are any positive quantities. Then $C=x+y-2xy=½+2ab$. Therefore x can not be less than ½ and y more than ½.

On the other hand, if $x=½-a$ and $y=½-b$, or if $x=½+a$, $y=½+b$; in either case $C\equiv x+y-2xy=½-2ab$. So that in these cases the cross over-ratio C is less than ½.

4. Conversely to 3, when the exchange ratios x and y are both less than ½, or when they are both more than ½, the cross-over ratio is less than ½.

That is, when $x<½$ and $y<½$, or when $x>½$ and $y>½$; in either case $C<½$. This was proved under 3.

5. When the cross-over ratio is greater than ½, one ex-

change ratio is less than $\frac{1}{2}$, the other greater than $\frac{1}{2}$. That is: If $C > \frac{1}{2}$, then $x < \frac{1}{2}$, $y > \frac{1}{2}$. This also was proved under 3.

6. Conversely to 5, when one exchange ratio is less than $\frac{1}{2}$, the other greater than $\frac{1}{2}$, the cross-over ratio is greater than $\frac{1}{2}$. That is: If $x < \frac{1}{2}$, $y > \frac{1}{2}$, then $C > \frac{1}{2}$. This also was proved under 3.

All these relations are evident in the table.

7. When the cross-over ratio is less than $\frac{1}{2}$, the two exchange ratios are either both equal to or less than the cross-over ratio; or both equal to or more than the complement of the cross-over ratio. They can not have any value lying between the cross-over ratio and its complement. That is: When $C < \frac{1}{2}$, either x and y each $\leqq C$ or x and y each $\geqq 1 - C$.

This is an extremely important principle, on which the final test of the theory depends. It is proved as follows:

In 3 we saw that if the cross-over ratio is less than $\frac{1}{2}$, either x and y are both less than $\frac{1}{2}$; or both of them are greater than $\frac{1}{2}$.

(*a*) Let us take first the case where x and y are each less than $\frac{1}{2}$. In this case, in the formula $C = x + y - 2xy$, the quantity $2xy$ is smaller than x, and smaller than y. For since x is less than $\frac{1}{2}$, 2x is less than 1, whence it follows that 2xy is less than y; and the same reasoning shows that 2xy is likewise smaller than x. Hence the formula for C subtracts from the sum of x and y a quantity smaller than y; it therefore leaves a quantity larger than x; and the same reasoning shows that it leaves a quantity larger than y. Only in the limiting case that $x = 0$ does $y = C$.

(*b*) Take next the other possible case, in which x and y are both greater than $\frac{1}{2}$. In this case $1 - x$ and $1 - y$ are both less than $\frac{1}{2}$. Thence it follows (by the reasoning just employed) that

$$(1 - x) + (1 - y) - 2(1 - x)(1 - y)$$

is greater than $1 - x$ and greater than $1 - y$. But, as was seen in (1),

$$(1-x)+(1-y)-2(1-x)(1-y)=x+y-2xy=C$$

So that in this case $C>1-x$ and $C>1-y$.

Thus the fraction C is nearer to 1 than the fraction $1-x$. If therefore we subtract the fraction C from 1, it will leave a smaller number than if we subtract the smaller fraction $1-x$ from 1. That is: $1-C<x$.

And in the same way it can be shown that $1-C<y$. Only in the limiting case that $y=1$ does $x=1-C$.

The general principle in this section can be expressed as follows:

When the cross-over ratio is less than ½, the two exchange ratios, x and y, either both differ from 0 by less than the cross-over ratio, or both differ from 1 by less than the cross-over ratio.

This relation is well seen in the table. For example, for the cross-over ratio .38 the two exchange ratios are either .3 and .2 (both less than .38), or they are .8 and .7 (both greater than .62, the complement of .38).

8. Conversely to 7:

If both exchange ratios, x and y, are less than ½, both are equal to or less than the cross-over ratio.

If both exchange ratios, x and y, are greater than ½, both are equal to or greater than the complement $(1-C)$ of the cross-over ratio.

9. When the cross-over ratio C is above ½, one of the exchange ratios (x) is equal to or less than the complement of the cross-over ratio $(1-C)$, while the other (y) is equal to or more than the cross-over ratio (C).

Or otherwise expressed:

When the cross-over ratio is above ½, one of the exchange ratios (x) differs from 1 by an amount equal to or more than the cross-over ratio, while the other (y) differs from 0 by an amount equal to or more than the cross-over ratio. That is, when $C>½$, $1-x \geqq C$, $y \leqq C$, or $x \leqq 1-C$, $y \geqq C$.

This can be proved by methods similar to those employed in 7.

10. Conversely to 9:

high or very low), they can not together give cross-over ratios of the more intermediate values. For example (as our table shows), if two factor pairs each give, with any other, cross-over ratios below .10, they can not give together a cross-over ratio lying anywhere between .18 and .84. If the two pairs each yield any cross-over ratios lying below .20, they can not give together a cross-over ratio lying between .32 and .68. These and many similar relations, illustrated in the table, are inherent in the theory we are considering, but are completely opposed to what is found in nature.

IV

These facts completely refute any theory which holds that the observed constant cross-over ratios between pairs of factors are the result of constant exchange ratios between the two members of a given pair—exchange ratios that are characteristically diverse for the different pairs (such theories as that outlined by Goldschmidt, 1917). The refutation is independent of the question of the nature of the forces involved; whatever the forces, if they give constant average exchange ratios for each pair, the results are bound to be inconsistent with the observed cross-over ratios. No theory will hold that does not provide for diverse relations between the different factors in the same chromosome, such that some tend to cling together more frequently than others.

Possibly some elements of the theory that diverse exchange ratios are characteristic for different pairs might be retained, if there be added provision for modification of the exchange ratio in a given pair, depending on whether or not exchange occurs in some other pair. It might be held, for example, that *A* and *a* are more likely to exchange if in the same cell *B* and *b* have exchanged; or the reverse. This would give a theory of mixed type, which added to the forces regulating the exchange between two members of a pair, other forces causing two given pairs to tend to do the same thing, or the opposite

thing. The "variable force" theory would therein approach the chiasmatype theory, in which the diverse relations between the factors belonging to different pairs are the primary, if not the exclusive, elements considered.

As theories of other type become successively modified so as to take into account the known facts: the fact that the chromosome actually is a linear aggregate; the fact that the two chromosomes while in this linear condition pair and intertwine; the fact that cross-overs occur only at the period when this occurs; the fact that two recessive allelomorphs when mated do not produce normals, while two recessives not allelomorphs do; the fact that after two factors, A and B, are found to hold together in one generation, if we mate their cross-overs *A–b* and *a–B,* we now find that it is *A* and *b,* not A and B that tend to hold together (Bridges, 1917); the fact that when a given factor is lost from a chromosome, others that have low cross-over ratios with that factor are also lost (Bridges, 1917*a*);—when the modifications required for bringing these facts into relation with each other and with others are introduced, it appears that the resulting theory will come more and more to resemble the chiasmatype theory. No theory is adequate that does not include and bring into relation the facts just mentioned, for a correct theory is nothing but a presentation of the facts in their correct (verifiable) relations.

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SHORTER ARTICLES AND DISCUSSION

NOTE ON THE COLORATION OF PLANES MINUTUS[1]

It is well known that the coloration of the grapsoid crab *Planes minutus*, a constant member of the Sargassum fauna, is "homochromic" to a high degree, not only as to tint and mottling, but also in the frequent occurrence of a blotch of pale yellowish or blank white upon the carapace; this has generally been supposed to be a mimicking of the white patches of encrusting bryozoa and *Spirorbis* tubes, which commonly infest the Sargassum.[2]. Experiments made to discover the extent of possible color changes in the adult *Planes* when it is placed over variously pigmented artificial bottoms have led to no result, other than to show—conformably with what is known for some other crustacea possessing a dense body pigmentation, as contrasted with a relatively scanty supply of well-scattered chromatophores—that the power of color adaptation is decidedly limited. It is, therefore, of interest to make record of an instance in which pronounced color adaptation of *Planes* had occurred in nature.

In January, 1916, after a rather severe gale, there was found stranded upon one of the reef "heads" at Bermuda a large "Spanish cedar" tree. It is certain that the tree had been in the sea for some time, as the surface layer was thickly populated by *Teredo* and boring amphipods. The trunk, the stumps of the roots and the submerged branches of the tree were covered with a forest of barnacles, *Lepas anatifera*, from among whose smoky-brown erectile peduncles were obtained a vast number of adult *Planes minutus* that were adhering to the more or less honeycombed parts of the exposed bark and wood. Without exception the crabs were deep brownish-red, save for the frequently occurring dorsal white patch. This pigmentation harmonized precisely in general tint with the mahogany-colored surface of the cedar tree.

The interest of this case lies in its demonstration that these crabs—prominent members of that specialized gulf-weed fauna which has been urged as part of an argument for the antiquity

[1] Contributions from the Bermuda Biological Station for Research, No. 84.

[2] *Cf.* Verrill, 1908, Pl. XIII; Murray and Hjort, 1912, p. 671, Pl. VI.

of the floating beds of Sargassum (Collins, 1917), probably for generations experiencing no other habitat than the gulf-weed—having yet retained a considerable capacity of color adaptation. Among Sargassum the hues of *Planes* vary considerably,[3] but the color of the present specimens was very much darker and redder than that of any I have seen described. The color agreement could hardly have resulted from a general staining of the crabs following ingestion of pigment derived from the tree, as the characteristic white blotch upon the dorsum was fully as well, if not somewhat more, developed in many of these specimens, than in the common ones living upon gulf-weed. Spectroscopic examination of alcoholic extracts of these crabs showed that the pigment was not detectably different from that of *Planes* taken on Sargassum. Whether the white patch represents in this instance an inherited tendency to lack of pigment on that area, or is rather to be regarded as (in addition) a mimicking of the white valves of the accompanying Lepads, is a question; the conspicuous development of the white shield, its large size and precise outline in more than 50 per cent. of the individuals, suggests the possibility of the latter alternative.

Presumably the floating cedar tree was invaded by *Planes* larvæ, which developed upon this dark reddish-brown substratum, and, like Hippolyte in the experiments of Gamble and Keeble (1900), produced there a pigmentation of corresponding appearance. In this way a coloration might be acquired which the crabs probably could not, at least quickly, have accomplished by adaptive color change in the adult state. No color changes were detected when these dark crabs were kept for six days upon Sargassum, in bright light.

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AGAR'S ISLAND,
BERMUDA

W. J. CROZIER.

[3] *Cf.* Murray and Hjort, 1912, Pl. VI.

THREE MUTATIONS IN PREVIOUSLY KNOWN LOCI

THREE mutations is the sex-chromosome have occurred in my cultures of *Drosophila melanogaster* (*ampelophila*). Two were reappearances of genes already known, namely, white and rudimentary; the third was the appearance of a new gene at the white locus and has been named coral, symbol w^{co}. In each case it is clear that the changes occurred in the wild type gene of a maternal chromosome. The evidence also indicates that the new gene arose relatively late in the history of the egg in each case, whereas if the mutation had occurred in the early oogonial stages several individuals with the new gene should have appeared. In cases where such information is known, it seems worth recording since it will make possible a later consideration of the relative stability of genes by a summing up of the frequency of mutations in the different loci.

As has been pointed out by Muller[1] recessive genes might exist for a long time before making an appearance, in case they were closely linked to a lethal. The character produced by the gene would ultimately be allowed to appear as the result of a cross over which would separate the gene and the lethal from the same chromosome. Previous to the time of crossing-over the character produced by the gene would never be seen, since all individuals pure for it would also be pure for the lethal and not survive. The gene could be indefinitely transmitted along with the lethal through heterozygous individuals. I mention this point because it is necessary in establishing the time of origin of a mutation to consider whether its appearance may be due merely to its recent separation from a lethal, which had obscured it. The three mutations dealt with here could not have been masked by a lethal because they were in the X-chromosome, and the presence of a lethal would have been apparent, as it would have produced a lethal sex ratio. No such lethal ratio has been found in connection with any of the three mutants either before or since their appearance. In these cases, then, it is safe to assume that the appearance of the first mutant marks the time of the mutation. If the mutation had occurred in earlier generations, several individuals bearing the character would have appeared instead of one.

In the case of the reappearance of a character, careful consideration must be given to the possibility of contamination, as has

[1] *Proc. Nat. Acad. Sci.*, Vol. 3.

been pointed out by Morgan and Plough.[2] This possibility has been taken into account and is discussed with reference to the appearance of each gene in that particular section.

ORIGIN AND DESCRIPTION OF CORAL

Coral arose in a mating of an eosin miniature bar-eyed male to a forked female with normal eyes. This female was a "secondary exception" from an XXY mother which had had no sex-linked eye color in her pedigree. Among 279 offspring that were of the expected classes and showed no lethal sex ratio, there was found about the middle of the count one heterozygous bar female which seemed to be "exceptionally" dark eosin. An eosin eye color in a female would be impossible to account for, since to be a female she must have obtained one of the mother's chromosomes, both of which carried normal red factors, as well as receiving the eosin bar chromosome of the father. A mating to one of her red-eyed brothers showed at once that the supposed eosin female was actually heterozygous for eosin and for a new allelomorph (coral) as she gave two kinds of sons, eosin and coral, while the daughters were eosin and the compound eosin-coral. The eosin-coral females are darker than pure eosin females and the original female was of this nature.

Coral is the seventh mutant allelomorph to be found in the white locus and counting the wild type gene forms with them a system of eight allelomorphs. In the order of their discovery these are: red, white, eosin, cherry, blood, tinged, buff and coral. Coral does not show bi-colorism, but is the same for males and females. It is similar to the color of very dark coral. It is darker than all the other members of this series with the possible exception of blood which according to the description of Hyde in his discussion of blood[3] shows a considerable variation of color according to cultural conditions. The color of coral is very close to the darker shades of blood, but is much darker than the lighter shades and does not show any such variations in range of color. Coral is distinctly darker than cherry and the other lighter members of this series. Coral is a dull color and does have the brightness of color of the wild stock, neither does it show the fleck in the eye.

The original coral female was re-mated to a white male from stock and behaved genetically, as would be expected on the as-

[2] AMER. NAT., Vol. 49.

[3] *Genetics*, 1, November, 1916.

sumption that coral was a member of the white allelomorphic series. The heterozygous white-coral compound in the female is intermediate in color between the two pure stocks. Coral is recessive to red. A coral male crossed to a yellow-white female gave all yellow-white sons and the intermediate (compound) white-coral daughters. Evidently the mutation took place in the wild-type gene of the mother, since it is that gene which did not occur in the daughter while the eosin gene of the father is retained. It also occurred near the maturation divisions as only one individual of the kind appeared. If the change had occurred in the early stages of the egg, it would probably have resulted in several of the offspring showing the new character.

Reappearance of White

In a cross of a bar male to a red-eyed female, which produced 251 offspring without a lethal sex ratio, one male was obtained which was white, although there was no white in the pedigree of either parent. This fly was found in one of the last counts of the bottle and had the appearance of being a young fly. Counts were made from the bottle every two days. Since I had no cultures going at that time which contained white and had had no white flies in my etherizing bottle previously, the fly can not be accounted for by assuming that it had remained in the etherizing bottle from a previous count of another bottle. It is highly probable, though not absolutely certain from these considerations that this white male was not due to contamination, but rather to a mutation in the wild type gene of a maternal chromosome. We may be sure that this change took place in the maternal chromosome rather than in that of the father, since males always receive their one X-chromosome from the mother except in relatively rare cases of non-disjunction, and in this case the male would have been bar.

In appearance the new white is not distinguishable from the white of the original stock and is quite without color in both males and females. Dr. A. H. Sturtevant has been testing the effect of various concentrations of alcohol in extracting color from the eyes of flies which are members of this multiple allelomorphic series and kindly added this new white to the material which he tested. He reported that the new white is acted upon exactly as is the original white. Genetic results showed the new white to behave as an allelomorph of the old. The new white male was crossed to a red sister and the offspring were all red.

The F_2 generation gave females all red and the males in equal classes of red and white, which is the genetic behavior expected for a sex-linked gene. To test whether this white was in the same locus as the old white, a white male of this stock was crossed to a yellow-white female from the original stock. The sons were yellow white and the daughters were white, not yellow, since yellow is recessive and was not carried by the father. No difference could be observed in eye color between either sex of the new white, or the daughters compounded from the two whites, and the males and females of the original white. It seems reasonable to conclude then that the white gene has reappeared by a second mutation from the red gene.

Second Origin of Gene for Rudimentary Wing

There appeared in a cross of an eosin miniature male to a broad, vermilion, forked female (both from stock cultures, all characters mentioned being sex linked) one son which was vermilion, forked like the mother, but which also had shortened wings. This wing character was later shown to be rudimentary. Crossovers in later generations showed that the maternal gene for broad was also present, but its effect was obscured by the rudimentary in all cases where both occurred together. This male so obtained and bearing genes for broad, vermilion, rudimentary and forked was outcrossed to a virgin wild type female to test whether the new character was of a genetic nature. The F_1 flies were normal in all respects. One pair of these produced 117 sons which were classified with respect to the characters vermilion, rudimentary and forked, while no attention was paid to broad, which did show in certain crossovers where it was separated from rudimentary. Out of 117 males, 3 were crossovers between rudimentary and forked, which gave a percentage of crossing-over of 2.6, whereas the value given by Morgan and Bridges[4] is 1.4 on the basis of a much larger number of flies. There were 27 crossovers between rudimentary and vermilion, which is a percentage of 22.2, while the above authors put it at 24.1. The nature of the crossovers obtained showed that the gene for the wing character was between vermilion and forked, which agrees with the assumption that it is a new appearance of rudimentary. The crossover values obtained are sufficiently near to expectation to justify this assumption in view of the small number of flies. Crosses were made to the stock rudimen-

[4] Carnegie Pub. No. 237, 1916.

tary to make sure that the new gene was at the rudimentary locus. Since homozygous rudimentary females show a high degree of sterility, the rudimentary stock is kept by crossing it to forked and using normal-winged females that are heterozygous for both rudimentary and for forked. One of the new rudimentary males was crossed to such a heterozygous female and the new rudimentary was shown to be an allelomorph of the old, as both rudimentary sons and daughters were obtained in practically equal numbers. The new rudimentary stock resembled the old as regards the sterility of the homozygous females. Miss C. J. Lynch in this laboratory tested several and reported that they showed the same high degree of sterility. Since the new character has the same appearance as old rudimentary, this seems to be merely the reappearance of that gene.

In this case it is clear that the change occurred in one of the maternal sex-chromosomes which already carried three sex-linked genes. The linkage relations of the new gene to these maternal genes make its origin in the maternal chromosome certain. Moreover, the male could have received his sex-chromosome only from his mother, as otherwise he would have been an XO male and would have been sterile.[5] The fly could not be accounted for on the assumption of contamination, as there are no flies of that particular constitution in the laboratory. The mutation was from the normal gene at the rudimentary locus. The appearance of only one individual indicates that the change occurred late in the history of the egg.

Summary

1. Two mutations have occurred at the white locus in the normal red gene, giving rise to a reappearance of white and to a new gene which produces an eye color called coral.

2. Coral is the eighth member of the multiple allelomorph series at the white locus.

3. Rudimentary reappeared as a change from the normal gene at that locus in a maternal chromosome.

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EVIDENCE FROM INSULAR FLORAS AS TO THE METHOD OF EVOLUTION

EVIDENCE as to the rôle which hybridization plays in evolutionary change may be obtained from various insular floras by a comparative study of the history of those plant types in them which are prevailingly self-fertilized and those which are prevailingly cross-fertilized, both as to the rapidity with which new local species are produced and as to the frequency with which old species disappear. With these points in view, analyses have been made of the vascular plants in the floras of eight islands or island groups: Ceylon, Mauritius, Socotra, New Zealand, Hawaii, Galapagos, Juan Fernandez and St. Helena.[1] In all these there is a conspicuous, often predominant, element in the flora which is strictly local or endemic, indicating that each island has been the theater of considerable evolutionary change.

Information is necessarily lacking as to the method of fertilization of most of the species, but our general knowledge of the reproduction of the higher plants allows us to divide them into three main types. The dicotyledons and petaliferous monocotyledons, possessing floral organs which in the great majority of cases are attractive to insects, are doubtless prevailingly cross-pollinated. In the glumaceous monocotyledons, on the other hand (chiefly Gramineæ, Cyperaceæ and Juncaceæ), the floral organs are not so constructed as to favor cross-pollination, and it will probably be agreed that crossing is much less common

[1] These analyses are based on the following authorities: Trimen, Handbook of the Flora of Ceylon; Baker, Flora of Mauritius and the Seychelles; Balfour, Botany of Socotra; Cheeseman, Manual of the New Zealand Flora; Hillebrand, Flora of the Hawaiian Islands; Stewart, Botany of the Galapagos Islands; Johow, Flora de las Islas de Juan Fernandez; Melliss, St. Helena; and Hemsley, Report on the "Challenger" Expedition: Botany.

among them than in the petaliferous types. Finally, in the vascular cryptogams, the very frequent occurrence of bisexual gametophytes seems to insure a still greater prevalence of self-fertilization.

The vascular flora of each island was divided into these three groups which were studied comparatively. Determination was first made as to the percentage of local or endemic species in each group. This degree of endemism provides us with a rough measure of the extent to which new forms have been developed on the island, and thus allows us to compare the rapidity of evolution in one floral group with that in the others.[2] In the following table are set forth the percentage of endemic species in each of the three main groups which we have mentioned, and for each of the islands:

TABLE I

PERCENTAGE OF ENDEMIC SPECIES IN VARIOUS FLORAL ELEMENTS

	Ceylon	Mauritius	Socotra	New Zealand	Hawaii	Galapagos	Juan Fernandez	St. Helena
Dicotyledons and Petaliferous Monocotyledons Average, 65%	35%	55%	42%	84%	84%	50%	73%	100%
Glumaceous Monocotyledons Average, 38%	11	14	9	56	60	30	37	87
Vascular Cryptogams Average, 23%	9	20	10	30	51	2	18	44

It is evident that the proportion of endemic species is much higher among those types which we have reason to believe are prevailingly crossed than among those which are prevailingly selfed, being highest among dicotyledons, lower among glumaceous monocotyledons and lowest among vascular cryptogams. The same fact appears among genera, for 95 per cent. of the endemic genera of these islands belong to petaliferous types and only 5 per cent. to the glumaceous monocotyledons and vascular cryptogams. These facts all point to the importance of hybridization as a factor in the production of new species.

The other aspect of evolutionary change, namely the disap-

[1] Of course not all the endemic forms can be regarded as of local origin, since certain of them may be isolated relicts of types formerly more widely spread. The proportion of these, however, which have not subsequently undergone specific change, and thus developed true local types, is probably small.

pearance of species, seems also to be influenced by the method of fertilization. Many of the genera which are themselves not endemic on any island are nevertheless represented there now *only* by endemic species. In such cases it seems clear that the first representative of the genus to invade the island has since disappeared there entirely and been replaced by local species. Table II gives the percentage of such genera (not endemic but represented only by endemic species) for each of the three plant types which we have discussed and for all the islands.

TABLE II

PERCENTAGE OF THE NON-ENDEMIC GENERA WHICH ARE REPRESENTED ONLY BY ENDEMIC SPECIES

	Ceylon	Mauritius	Socotra	New Zealand	Hawaii	Galapagos	Juan Fernandez	St. Helena
Dicotyledons and petaliferous monocotyledons. Average, 42 %	9%	28%	29%	44%	57%	16%	52%	100%
Glumaceous monocotyledons. Average, 26 %	2	11	12	10	40	11	38	83
Vascular cryptogams. Average, 10.5 %	3	0	0	20	18	0	19	25

It is evident that genera in which the "original species" has become extinct are proportionally commonest among dicotyledons, less common among glumaceous monocotyledons and rare among vascular cryptogams, thus suggesting that hybridization has resulted in the "swamping out" of the early forms. If local adaptation and natural selection alone were at work, it is hard to see why extinction should not be equally common in all these groups. The facts point to the importance of hybridization in completely altering specific type when a group of individuals have been isolated from the main body of the species.

Against the soundness of these conclusions several points may be urged. Vascular cryptogams are perhaps inherently less variable and quick to produce new species than flowering plants. It may be, too, that cross-fertilization is much more common among them than is generally believed. Whether the recognized "species" among these plants is the equivalent of the "species" among angiosperms, or is a much more inclusive group, is also a matter of doubt. These points can not well be brought against the glumaceous monocotyledons, however, as contrasted with the petaliferous types. Whatever its interpretation, the fact seems

clear that among dicotyledons and petaliferous monocotyledons new types are produced and old types lost much more quickly than anywhere else in vascular plants, a fact which in the light of our knowledge of methods of reproduction certainly supports the view that hybridization has been a powerful factor in evolutionary change.

Summary

Evidence from a comparative study of endemism in various elements of certain insular floras tends to show that among cross-fertilized types new species are developed more rapidly and old ones lost more frequently than among self-fertilized types, thus emphasizing the importance of hybridization as a factor in evolutionary change.

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A LAND PLANARIAN FOUND AT BERMUDA[1]

In 1902 Professor Verrill recorded ("The Bermuda Islands," p. 436, Fig. 237), that there had been reported to him the finding at Bermuda of a "worm" which appeared to be a land planarian. With the possible exception of this worm, which may have been a *Bipalium,* no land planarians have been seen at Bermuda. While collecting earthworms, in September, 1917, I obtained among moist decaying leaves in a "fertilizer pit" at Point Shares, Pembroke Parish, a single specimen of a flatworm which seems to be a species of *Geoplana.* The "pit" was in use as a dumping ground for garden refuse, and since no land planarians appear to be native to Bermuda, the worm may have been introduced in company with plants. It was 50 mm. long and 2 mm. wide, pale greenish blue on the ventral surface,—which bore a rather small oral sucker in the usual position,—the ground color of the dorsal surface being a deeper shade of the same greenish blue, but marked with two deep blue or black longitudinal stripes running the whole length of the animal. Two well-developed pigment spots were present, one on either lateral margin of the anterior end. It is not impossible that this species might become permanently colonized at Bermuda (although no other specimens have been found), and this note may therefore be of use in fixing the date of its earliest observed appearance.

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[1] Contributions from the Bermuda Biological Station for Research, No. 85.

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THE RÔLE OF REPRODUCTION IN EVOLUTION[1]

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THE establishment of methods of reproduction which maintain variation and inheritance mechanisms on a high plane of efficiency is naturally a fundamental requirement in organic evolution. Since, however, inheritance mechanisms presumably equivalent are common to every method of reproduction, one should be able to interpret the evolutionary tendencies in the matter by comparing their effectiveness in offering selective agencies their raw material. Some will hold this statement to be a self-evident truth; others may maintain as strongly either that the premises are wrong or that the conclusion is not justified even if the premises be granted. Perhaps it is safer to ply the middle course; if the case is not so obvious as a Euclidian axiom, as a compensation rigorous proof may be less difficult.

As a basis for argument, let us sketch the general trend of reproductive evolution in plants and animals.

Ordinarily, one speaks of two types of reproduction among organisms, asexual and sexual. This is a convention that has taken on the dignity of a "folkway" among biologists. Its employment should imply assent to the proposition that the varied forms in which each of these classes presents itself are inherently equivalent, and that

[1] Read by title at the Symposium of the American Society of Naturalists on the subject "Factors of Organic Evolution," Jan. 5, 1918.

the groups considered as units are fundamentally distinct, but it is doubtful whether any such implication would be admitted by the majority of its users. In fact one could hardly maintain that simple division, sporification, the production of gemmules, true budding, fragmentation with regeneration of parts, and the various kinds of apogamy and parthenogenesis on the one hand, and all nuclear fusions on the other, can be grouped together as if they are of the same evolutionary value, if this term be used in any narrow or special sense; but from a broader viewpoint, the conventional classification has a real and deep meaning which perhaps the biologist has grasped instinctively.

There are both asexual and sexual methods of reproduction in nearly all groups of animals and plants; among animals the second has almost supplanted the first, among plants the two have continued side by side. In neither kingdom was sex developed as a more rapid means of multiplication, since, as Maupas showed, a single infusorian may become the progenitor of some 50,000 individuals during the time necessary for one pair to conjugate. Some other requirement was fulfilled; and fulfilled adequately if we may judge by the number of times sexual differentiation arose and the tenacity with which it was retained.

Just when sexual reproduction first originated in the vegetable kingdom is still a question. Among the lower forms only the schizophytes, flagellates and myxomycetes have passed it by. Perhaps it is for this reason that these forms have remained the submerged tenth of the plant world. It is tempting, as Coulter (1914) says, to see sex origin in the Green Algæ. There, in certain species, of which *Ulothrix* is a good example, spores of different sizes are produced. Those largest in size germinate immediately under favorable conditions and produce new individuals. Those smaller in size also germinate and produce new individuals, but these are small and their growth slow. Only the smallest are incapable of

carrying on their vegetative functions. These come together in pairs. Two individuals become one as a prerequisite to renewed vigor. Vegetative spores become gametes. Something valuable—speed of multiplication—is given up for a time that something more valuable in the general scheme of evolution may be attained.

This is indeed an alluring genesis of sex. Let us use the indefinite article, however; no doubt it is *a* genesis of sex, but it can hardly be *the* genesis of sex. Various manifestations of sex are present in other widely separated groups of unicellular plants, the Peridineæ, the Conjugatæ and the Diotomeæ—the Conjugatæ being indeed the only great group of plants in which there is no asexual reproduction. In these forms one can not make out such a good case of actual gametic origin, but the circumstantial evidence of sex development in parallel lines is witness of its paramount importance.

After the origin of sex, many changes in reproductive mechanisms occurred in plants, but almost all of them resulted merely in greater protection of the gametes, in increased assurance of fertilization, or in provision for better distribution. First there was a visible morphological differentiation of gametes, the one becoming a large inactive cell stored with food, the other becoming small and mobile. Then came the evolution of various sex organs, and finally the alternation of generations. In the higher plants a long line of changes have occurred connected with the alternation of generations; the spore-producing type has developed from a form of little importance to that which dominates the vegetable world, the gamete-producing type has degenerated until it consists of but two or three cell divisions. In these variations there is reproductive insurance, something which also may be said of those manifold adaptations which provide zygotic protection either in the seed or the adult plant, but they are no more direct changes in reproductive mechanism than are the diverse means which arose to secure dispersal. In fact in all of these changes no new

process of fundamental evolutionary significance occurred, unless it be the various mechanisms devised to promote or to insure cross-fertilization, and which may be interpreted as variations tending to perfect sexuality.

Coincident with the general trend of plant evolution just mentioned, two important changes in the nature of retrogressions occurred, which have persisted in many species. A new type of asexual propagation arose, apogamy, which though it appeared under several guises, apogamy in the narrow sense, parthenogenesis and polyembryony, is none the less asexual reproduction returned under another name and apparently with no particular advantages over the older types. Further, hermaphroditism was developed and has persisted in numerous lines. We may be wrong in calling hermaphroditism a retrogression, for it has the great advantage of a certain economy of effort in the production of gametes, but nevertheless it is certainly a change which *per se* is in the opposite direction from that established when sex was first evolved. A moment of consideration not only makes this clear, but gives us a pretty satisfactory proof that the gain made when continuous multiplication was halted for a time by the intervention of a fusion at the genesis of sexual reproduction was in some way connected with the mixture of dissimilar germplasms. This conclusion is hardly avoidable from the fact that although hermaphroditism retained the cell fusion mechanism of gonochorism it was still necessary for Nature to evolve means for cross-fertilization. And the multitude of ways in which she solved this problem must mean that an immense advantage was secured.

In spite of the great morphological differences between animals and plants, the essential evolutionary changes affecting reproduction in the two kingdoms have been so similar as to be almost uncanny. Accepting the division of animals into twelve phyla as recognized by many modern zoologists (Parker and Haswell), one finds the following facts regarding reproduction. Asexual repro-

duction in the narrow sense is common in Protozoa, Porifera, Cœlenterata and Platyhelminthes, and is sporadic in Molluscoida, Annulata, Arthropoda and Chordata. If fragmentation and regeneration be included, Echinodermata and possibly Nemathelminthes are added. If parthenogenesis is included, Trochelminthes is admitted. Thus only the Mollusca have no form of asexual reproduction, and zoologists would hardly feel safe in maintaining its absence there since the life history of so many forms is unknown. This being the case, one must admit that asexual reproduction has been found satisfactory for most of the great groups of animals as far as actual multiplication is concerned. For other reasons, however, it evidently did not fulfill all requirements, since sexual reproduction is established in every phylum. Further, omitting the Protozoa in which it is difficult to decide such sexual differences, gonochorism is present everywhere except in the Porifera, and hermaphroditism everywhere except in the Trochelminthes, although in Nemathelminthes, Echinodermata and Arthropoda it is rare.

Now if our conclusions regarding the true rôle played by sex in evolution are correct, hermaphroditism is a secondary and not a primitive phenomenon. In this we follow Delage, Montgomery and Caullery rather than the majority of zoologists. We believe it to be the only logical view in spite of the fact that the Porifera, usually considered so unspecialized, are all hermaphroditic. Perhaps the Porifera are farther along in specialization than is admitted, for to find the substance nearest chemically to the so-called skeleton of the sponges one must turn to the arthropods (the product of the spinning glands of certain insects). Hermaphroditism, therefore, as in plants, is from this viewpoint a regression. And as in plants it was not found adequate. In giving up diecism for monecism, something was lost, and this something had to be regained by further specialization. Hence, even as in the vegetable kingdom one finds the essential feature of bisexuality, mechanisms providing for mixtures of dif-

ferent germplasms, restored by means of protandry, protogyny or self-sterility.

In even such a brief consideration of the more important changes which have occurred in the reproductive mechanisms of animals and plants, one thing stands out impressively. Both animals and plants have adopted as the most acceptable and satisfactory modes of reproduction, methods which are identical in what we deem to be the essential features, something that can be said of no other life process. These significant features are the preparation of cells which in general contain but half of the nuclear material possessed by the cells from which they arise, which are differentiated into two general classes that show attraction toward each other, and which will fuse together in pairs to form the starting point of a new organism. This parallel evolution is of itself valid evidence of the importance of the process. Let us return to our original proposition for its interpretation.

First, is there any evidence that sexual reproduction differs from asexual reproduction in what may be called the heredity coefficient? In other words, does one method hold any advantage over the other as an actual means for the transmission of characters? I have answered this question in the negative, but it must be confessed that the basis for this answer is a long and intimate experience in handling pedigree cultures of plants rather than the study of a large amount of quantitative data bearing directly on the problem. Quantitative data are to be found, of course, and plants furnish the best material because of the ease in handling large numbers of both clons and seedlings side by side; but even with the best of plant material, several undesired variables are present. Practically the inquiry must take the form of a comparison between the variability of a homozygous race when propagated by seeds and when propagated by some asexual method. The first difficulty is that of obtaining a homozygous race and thus eliminating Mendelian recombination. The traditionally greater variability of seed-propagated

strains is due wholly to this difficulty, I believe. It may be impossible to obtain a race homozygous in all factors. There may be a physiological limit to homozygosis even in hermaphroditic plants. The best one can do is to use a species which is naturally self-fertilized, relying on continued self-fertilization for the elimination of all the heterozygous characters possible. I have examined many populations of this character in the genus *Nicotiana* and have been astounded at the extremely narrow variability they exhibit. Even though one can not grow each member of such a population under identical conditions as to nutrition, the plants impress one as if each had been cut out with the same die. Qualitative characters such as color show no greater variation, as far as human vision may determine, than descendants of the same mother plant propagated by cuttings. Further, in certain characters affected but slightly by external conditions, such as flower size, the sexually produced population not only shows no greater variability than the asexually produced population, but it shows no more than is displayed by a single plant. Yet one must remember that in such a test the seeds necessarily contain but a small quantity of nutrients, and for this reason the individual plants are produced under somewhat more varied conditions than those resulting from cuttings, hence it would not have been unreasonable to have predicted a slightly greater variability for the sexually produced population even though the coefficient of heredity of both were the same.

I have made similar though less systematic observations on wheat—an autogamous plant almost as satisfactory for such a test as *Nicotiana*—with practically identical results. I do not know of any published data on the subject, however, taken either from these or any other plants. In fact, there are few other plants from which data could be obtained with so little likelihood of experimental error.

On the other hand, zoology has furnished a considerable amount of such evidence (*cf.* Casteel and Phillips,

1903; Kellogg, 1906; Wright, Lee and Pearson, 1907). One need only mention Kellogg's work on bees as a type. Kellogg assumed that if amphimixis were the principal cause of the continuous variations postulated by Darwin and Weismann as the most important source of material for the use of the natural selection,[2] parthenogenetically produced individuals should be less variable than those produced sexually. A statistical investigation showed, however, that the characters of drones probably are more variable than those of worker bees of the same race. Since Kellogg believes Darwin's judgment that "males vary more than females" to have been disapproved, he concludes that "amphimixis is not only not necessary in order to insure Darwinian variation, but there is no evidence (that I am aware of) to show that it increases variation."

It is hardly necessary to point out here the numerous mathematical and biological pitfalls which should be considered before one could accept as valid the statistical differences that appear to exist when coefficients of variation based on such data are examined. It should suffice to note that the researches of Wright, Lee and Pearson (1907) on wasps of the species *Vespa vulgaris* showed just as great a difference in variability between workers and drones in favor of the former. Apparently, the statistics in these two nearly related groups lead to opposite conclusions; in reality probably neither statistical difference is significant as far as the question we are discussing is concerned. The only conclusion justified by such data would seem to be that the coefficient of heredity is as high in the production of asexual as it is in the production of sexual forms.

Moreover, one can not expect anything more definite from this method of attack. Biologists may differ as to

[2] It should be noted here that all parthenogenetic eggs are not mere spores. Some preparation often occurs through the emission of one polar body. This may be merely a kind of recapitulation, a vestigial process no longer having any significance whatever, but since we are not certain it seems to the writer that the evidence from plants at present must be regarded as stronger.

the definition of fluctuation, mutation, etc., but they are generally agreed that germinal variations, be they great or small, are in most species so rare they can not be gauged by the use of ordinary statistical methods. For this reason, a comparison between the variability of the drones and of the workers of a pure race of bees is not likely to show any difference between these two modes of reproduction in the matter of the frequency or the type of the germinal variation produced, and can not answer the question as to whether sexual reproduction contributes more material for the use of natural selection than asexual reproduction. A study of variability in crossed races, where the effect of Mendelian recombination can be considered, would be a more logical attack upon the second problem, but is hardly necessary in view of the other evidence available.

One is then justified in claiming there is no experimental evidence to show that sexual reproduction in itself is not an exact equivalent of asexual reproduction in the matter of a heredity coefficient, but is this also true for germinal variation? We believe it is. Variations there are in both asexual and sexual reproduction, but it can not be maintained that they occur more frequently in the latter. There are insects in Oligocene amber apparently identical with those of to-day, proving that constancy of type is possible through long periods of time under sexual reproduction; yet germinal variations occur to-day in somewhat noteworthy numbers, as Morgan's work on *Drosophila* shows, although the proportion of these variations which show possibilities of having an evolutionary value, as evidenced by persistence in natural types, is probably small. On the other hand, the number of variations produced under the dominance of asexual reproduction can not be said to be less numerous, even among organisms of a relatively high specialization. If there are those who doubt this statement, let them refer to the immense list of bud-variations in the higher plants compiled by Cramer (1907).

There would be little reason in pushing the claims

further, since even though there does not seem to be a sufficient difference between sexual and asexual reproduction in the matter of variation frequency to make it a subject of experimental proof, certain theoretical points raise the suspicion that there is such a difference. All we would maintain is that to account for the general persistence of sexual reproduction by such a cause, the difference in its favor should be so great that it could easily be determined experimentally. Since this is not true, we believe the hypothesis should be discarded.

The points of theory referred to are these. It will be allowed by all that there is some considerable evidence of the chromosomes being the most important conservators of hereditary factors—the physical bases of heredity in whatever form they may be. If it is assumed then that changes in constitution in these cell organoids are followed by changes in type, and that such changes in constitution are equally probable in all chromosomes, it follows that parthenogenetic individuals having the haploid number of chromosomes should show a larger proportion of germinal variations than members of the same species having the diploid number of chromosomes, because variations of all kinds should be recognizable in the former case, while in the latter, recessive variations could not be detected until the first or second filial generation, and then only when the proper mating was made. There is some evidence that this reasoning is not wholly improbable. But variations occur much more frequently in heterozygotes than in homozygotes. To me this simply means that bud-variations *are detected* more frequently in heterozygotes than in homozygotes: and an interpretation is not hard to find. Retrogressive variations are much more frequent than progressive variations, and a retrogressive variation in a particular character shows only when the organism is heterozygous for that character. If a retrogressive bud-variation arises in a homozygote and gametes are afterwards developed from the sporting branch it is not at all unlikely that the variation may show in the next generation, but it will be attributed then to

gametic mutation. If one compares asexual and sexual reproduction from the standpoint of frequency of variation only, then sexual reproduction may seem to hold the advantage over asexual reproduction in the usual sense; but parthenogenesis, which is certainly a form of asexual reproduction, is in theory better adapted than sexual reproduction for giving large numbers of variations.

If, therefore, one is constrained to agree that the bulk of the evidence points to a practically identical coefficient of heredity for both forms of reproduction, and that variation in the sense of actual changes in germinal constitution *may* occur with greater frequency in asexual reproduction, if there is any difference at all between the two forms, he is driven either to the conclusion of Maupas that continued asexual reproduction is impossible through some protoplasmic limitation or to the conclusion of Weismann that a mixture of germplasms offers sufficient advantages to account for everything. This is the dilemma[3] unless one wishes to maintain that efficient mechanisms for nutrition, adaptation, protection and distribution could not be evolved or maintained under asexual reproduction.

The contention of Maupas can not be dealt with experimentally any more successfully than the question as to the inheritance of acquired characters since experimental time and evolutionary time are not of the same order of magnitude. The long-continued experiments of Woodruff in which vigorous strains of paramecium have been kept dividing asexually for several thousand generations, however, as well as the botanical evidence that numerous species having no sexual means of multiplication have continued to exist during long periods of time, weight the balance against him. One need not hesitate to concede that all of these organisms are rather low unspecialized types; the modern development of genetics has built up such a solid structure in favor of Weismann's view that there is little need of argument along the older line.

[3] Naturally another hypothesis wholly new to biology may be submitted at any time.

The main argument in favor of Weismann's viewpoint does not take long to state. It is this: Mendelian heredity is a manifestation of sexual reproduction. Wherever sexual reproduction occurs, there Mendelian heredity will be found. The very fact that it describes the sexual heredity of both animals and plants is sufficient proof of its generality in this regard. Now if N variations occur in the germplasm of an asexually reproducing organism, only N types can be formed to offer raw material to selective agencies. But if N variations occur in the germplasm of a sexually reproducing organism 2^n types can be formed. The advantage is almost incalculable. Ten variations in an asexual species mean simply 10 types, 10 variations in a sexual species mean the possibility of 1,024 types. Twenty variations in the one case is again only 20 types to survive or perish in the struggle for existence; 20 variations, in the other case, may present 1,032,576 types to compete in the struggle. It is necessary to hedge the argument by pointing out that these figures are the maximum possibilities in favor of sexual reproduction. It is improbable that they ever actually occur in nature, for 2^{20} types really to be found in the wild competing for place after only 20 germinal variations would mean an enormous number of individuals even if the 20 changes had taken place in different chromosomes, and if the variations were linked at all closely in inheritance the number required would be staggering. But there are breaks in linked inheritance, and the *possibility* is as stated.

These advantages remain even though it should be shown later that the more fundamental and generalized characters of an organism are not distributed by Mendelian heredity. Loeb (1916) believes that the cytoplasm of the egg is roughly the potential embryo and that the chromosomes, distributed as required by the breeding facts of Mendelian heredity, are the machinery for impressing the finer details. There is something to be said for this point of view, though at present it is but a working hypothesis. But granting its truth it does not detract from the advantages gained by sexual reproduction. Even the most

strict mutationist would hardly maintain that evolution in general has come about through tremendous changes involving sterility between the mutant and the parent types. It seems unnecessary to deny such possibilities; but the weight of evidence is in favor of the majority of variations being comparatively small, changes in detail, the very kind which are known to be Mendelian in their inheritance.

Yet sexual reproduction in itself does not assure these advantages, though they are based upon it. There must be means for the mixture of germplasms. This opportunity was furnished originally by bisexuality. Then came hermaphroditism, manifestly an economic gain, yet on the whole unsuccessful except as functional bisexuality was restored by self-sterility, protandry, protogyny or mechanical devices which promoted cross-fertilization.

The prime reason for the success of sexual reproduction then, as Weismann maintained, is the opportunity it gives for mingling germplasms of different constitution and thereby furnishing many times the raw material to selective agencies that could possibly be produced through asexual reproduction. Further, there are three minor advantages which rest upon the same mechanism. They are minor advantages only when compared to the major, and should not be passed by.

Let us first consider heterosis, the vigor which accompanies hybridization. This phenomenon has long been known. It is characteristic of first generation hybrids both in the animal and vegetable kingdoms. It affects the characters of organisms in much the same manner as do the best environmental conditions. In other words, the majority of characters seem to reach the highest development in the first hybrid generation. The hybrid individual therefore holds some considerable superiority over the individuals of the pure races which entered into it, and is thereby the better enabled to survive and to produce the multiplicity of forms which its heterozygous factors make possible. The frequence of this phenomenon, for it is almost universal, together with the fact

that it seems impossible to fix the condition, led Shull and the writer independently to the conclusion that certain factors in addition to their functions as transmitters of hereditary characters also had the faculty of carrying some sort of a developmental stimulus when in the heterozygous condition. The recent work of Morgan on linked characters, however, makes it possible to give another interpretation, as Jones (1917) has demonstrated. If it be assumed that several variations have occurred in each of one or more chromosomes, then it can be shown that the first-generation hybrid between such a variant and the race from which it arose will bring together all dominant or partially dominant characters. In the second hybrid generation, on the other hand, Mendelian recombination steps in and makes it improbable that many individuals shall have such a zygotic composition. And only in the rare cases where the proper breaks in linkage have occurred can a homozygous individual of this type be produced.

The latter hypothesis holds the advantage that it furnishes hope for a homozygous combination as valuable as that of the first hybrid generation no matter how rarely it may be assumed to occur, but whether it holds for the majority of organisms or not may depend on a future decision as to the frequency of side-by-side synapsis as compared to end-to-end synapsis. Our knowledge of linkage rests almost entirely on Morgan's work on *Drosophila* where side-by-side synapsis occurs at the maturation of the germ cells. If the break in linkage between groups of characters apparently carried by a single chromosome, which Morgan finds to be so exact in *Drosophila,* should actually depend on Jannsen's theory of chromosome, twisting at synapsis, then some other type of inheritance may be found in species having end-to-end synapsis. Perhaps this is the reason why the Œnotheras have such a peculiar heredity, for in them Davis (1909) thinks end-to-end synapsis prevails. But, be this as it may, the vigor of first generation hybrids is a fact and not a theory, and the advantage it brings to the hetero-

zygotic individual in competition with its fellows can not be gainsaid.

The investigations of Shull and of the writer on the effects of cross- and self-fertilization have brought to light another series of facts with a bearing on the problem under discussion. It has been shown that the apparent deterioration of cross-bred species when self-fertilized is in large measure and perhaps wholly due to the loss of hybrid vigor[4] through the formation of homozygotic Mendelian recombinations and not an effect of inbreeding *per se* because of the union of like germplasms. This is a plausible argument against Darwin's idea that continued inbreeding is abhorrent to Nature. It may even be said to be a valid reason for declining to accept Maupas's belief in the impossibility of continued asexual reproduction, for there is no very good reason for distinguishing between continued asexual propagation and continued self-fertilization. Inbreeding simply brings about the opposite effect from crossing, and we can see no reason for the comparative failure of naturally inbred types in the wild other than the lack of chances for progress. The one is the conservative manufacturer who continues the original type of his article, the other is the progressive who makes changes here and there without discouragement until the acceptable improvement is found. In fact, if this argument be overlooked, the inbred types which have persisted hold some advantages over the cross-bred types. The self-fertilized species are inherently strong and vigorous, witness tobacco and wheat. They stand or fall on their own merits. They are unable, as are cross-bred species, to cover up inherent weakness by the vigor of heterozygosis. Cross-fertilized maize has become the king of cultivated plants because of its variability, but many of our best varieties carry recessive characters very disadvantageous to the species.

The next secondary advantage of sexual reproduction is

[4] Accepting the view that the vigor of the first hybrid generation is due to dominant characters meeting makes this argument even more forcible.

the division of labor made possible by secondary sexual characters, using the term very generally and including even such differences as those which separate the egg and the sperm. It is not known just how these differences arose or by what mechanism they are transmitted. The greatest hope of reading the riddle lies in an investigation of hermaphroditic plants, for there are technical difficulties which seem to preclude their solution in animals. For example, breaks in the linkage between sex-linked characters occur only in the female in *Drosophila,* and as the sex chromosome is double in the female, it can not be determined whether the differentiation between male and female is due to the whole chromosome or not. But this ignorance does not give reason for a denial of the great advantage which sexes bearing different characters hold over sexes alike in all characters except the primary sex organs.

The only glimpse of the truth we have on these matters comes from recent work on the effect of secretions of the sex organs on secondary sexual characters. The effect of removing the sex organs and the result of transplanting them to abnormal positions in the body have shown that in vertebrates the secretions of these organs themselves activate the production of the secondary sexual characters. This does not seem to be the case in arthropods, however, so one can not say that primary sexual differentiation and secondary sexual differentiation is one and the same thing.

Finally there is a presumable advantage in gonochoristic reproduction in having sex-linked characters. We say presumable advantages, for all of the relationships between sex and sex-linked characters are not clear. The facts are these: One sex is always heterozygous for the sex determiner and the factors linked with it. Now it may very well be that there is an actual advantage in the heterozygous condition, as we have seen above. But should the so-called vigor of heterozygosis prove to be only an expression of the meeting of dominant characters, still a possible advantage accrues to this phenomenon be-

cause the mechanism contributes toward mixing of germ-plasms. As an example, let us take the *Drosophila* type of sex determination. There the sperm is of two kinds: the one containing the sex chromosome and its sex-linked factors, the other lacking it. The eggs are all alike, each bearing the sex chromosome. It follows then that the male *always* receives this chromosome from his *mother*, who may have received it from *either* her *father* or *mother*. Moreover, further variability may be derived from the linkage breaks which occur always in the female. This last phenomenon is hardly worthy of special mention, however, until it is shown to be typical of such reproduction.

This short reconnaissance presents the pertinent facts in the situation as they appear to the writer. A very great number of interesting things connected with reproduction during the course of evolution have not been mentioned. This is because it is felt that the essential feature of the rôle of reproduction in evolution is the persistence of mechanisms in both the animal and plant kingdoms which offer selective agencies the greatest amount of raw material. Other phenomena are wholly secondary.

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CONTINUOUS AND DISCONTINUOUS VARIATIONS AND THEIR INHERITANCE IN PEROMYSCUS. II

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IV. Heredity of the Racial Differences

In view of the long-recognized correlation between certain of these subspecific characters—namely, those relating to pigmentation—and certain factors of the physical environment, the possibility has suggested itself that the characters in question might be purely "ontogenetic," *i. e.*, produced anew in each generation by the action of external physical factors. The simple experiment of transplanting mice from one habitat to another has disposed of this suggestion.

As I have more than once reported elsewhere (1915*a*, 1917, 1917*b*) entirely negative results have been reached, so far as climatic influences are concerned. Neither the transference of the desert race to Berkeley, nor the transference of both the desert and the redwood races to La Jolla have resulted in any demonstrable change, at least up to the third cage-born ("C_3") generation.

The La Jolla test is the more satisfactory of the two, since the number of animals employed is very much greater. Thus far, however, only the C_2 animals (38 *rubidus* and 96 *sonoriensis*) have been killed, measured and (in part) skinned. The C_3 generation is still kept alive for breeding purposes, but the characteristic racial differences are obvious. On comparing the skins of the palest and the darkest *rubidus*, or the palest and darkest *sonoriensis* of the C_2 generation, with the extremes among the wild grandparents, it will be seen that the range of color variation has not appreciably changed.

Not only are the larger color differences which distinguish these main races heritable, but certain lesser differences which distinguish narrowly localized sub-races have been shown to be genetic characters. In a recent paper (1917) I discussed an aberrant colony of "*rubidus*" inhabiting an isolated sand-spit fronting on the ocean.[15] The evidence for the inheritance of these peculiarities of color may now be stated somewhat more strongly than was done in that paper. Upon preparing the skins of the three C_1 members of this sub-race, born and reared at La Jolla, it was found that *all three* were of the aberrant hue.[16]

As regards differences relating to the measurable parts, certain preliminary explanations are necessary. It was early found that the cage-born mice depart from the wild type in certain rather striking respects. They are, on the average, considerably smaller than the latter, and have tails, feet and ears which are shorter not only absolutely but relatively. In extreme cases these malformations may fitly be termed deformities. Not rarely, too, the dorsal tail-stripe becomes so diffuse that definite outlines can no longer be distinguished. Measurements reveal the fact that this stripe becomes narrower, on the average, in the cage-born animals. Furthermore, the fertility of the captive generations is greatly reduced.

These abnormal characteristics resulting from captivity are manifested much more strongly by the Eureka race than by the desert one, or by the race which is native to this locality (La Jolla). In fact, my original stock of *rubidus*, consisting of over a hundred animals of the wild generation, has dwindled down to one male and six females in the C_3 generation. In contrast to this, no diffi-

[15] I there neglected to point out the analogy between this race and that described by Bangs (see Osgood, 1909, p. 121) from the island of Monomoy, Massachusetts. Castle and Phillips, as I learn from Dr. Castle, have bred this form in the laboratory and found its peculiarities to be "really genetic." Morgan's findings (1911) in respect to this question appear to have been complicated by the appearance of artificially induced abnormalities.

[16] In my earlier statement, based upon the appearance of the living animals, it was said that two of the three were exceptionally pale.

culty has been found in maintaining approximately the original numbers of the other two races, despite the sterility of a large proportion of the individuals. Here, then, we may note in passing, is another interesting racial difference of a physiological nature.

This deterioration of the stock, it must be pointed out, is progressive. Each generation probably presents more abnormalities than the preceding one. The causes of this condition are at present entirely unknown to me. Malnutrition or intoxication, resulting from pathogenic bacteria or protozoa in the alimentary canal, may be mentioned as possibilities. Many of the animals are now being reared in small open pens, where they are allowed to burrow in the ground. A preliminary test of this plan encourages us to hope that the troubles referred to may thus be avoided.

The following table presents mean values for certain characters in the C_2 generation, for the three races which are now being reared at La Jolla.

TABLE V

	Sex	No. of Cases	Body (Mm.)	Tail (Per Cent.)	Foot (Mm.)	Ear (Mm.)	Tail-Stripe (Per Cent.)
Eureka	♂	21	85.5	93.1	20.26	16.39	37.3
	♀	13	87.2	91.5	20.30	16.90	39.5
La Jolla	♂	61	87.4	79.6	19.62	17.66	30.7
	♀	43	89.4	79.1	19.56	17.74	31.1
Victorville	♂	45	85.3	75.6	18.65	16.43	25.9
	♀	49	87.0	74.8	18.81	16.90	26.2

It is plain from this table that, in respect to the four characters other than body length (tail length, foot length, ear length and tail-stripe), the three races have maintained the same relative positions in the series as formerly. When arranged with reference to tail, foot and tail-stripe, the series, as before, is: Eureka > La Jolla > Victorville. As regards ear length, the earlier arrangement likewise holds, viz.:

$$\text{La Jolla} > \begin{cases} \text{Eureka,} \\ \text{Victorville.} \end{cases}$$

Another significant fact does not appear from the foregoing table, however. The modifications of the three

races, indicated by the consistent reduction of all these values, has not affected them to an equal degree. In respect to all four of the characters (body length not here considered) the local (La Jolla) race has been least modified, while in respect to three of them (tail length, tail-stripe and ear) the Eureka race has been most modified. Thus there has been a mean reduction of 11 per cent. in the tail length of *rubidus*, 7½ per cent. in that of *sonoriensis*, and only 5 per cent. in that of *gambeli*. There is, therefore, a convergence between the Eureka and the La Jolla races, and if I had only these two under comparison, I might have been disposed to conclude that local conditions had brought about a modification of *rubidus* in the direction of *gambeli*. But the case of *sonoriensis*, which actually diverges farther from the local race in the C_2 than in the parent generation, shows that this explanation is not the correct one. These differences in the degree of modification are probably indices of the susceptibility of these three races to the malign influences of captivity, which have already been discussed. In harmony with this view is the fact that the Eureka mice are likewise far less fertile, under local conditions, than either of the other races.

V. Heredity of Individual Differences within Each Race

It has been shown that a wide range of individual variability occurs within each race in respect to just those characters by which one of these groups is distinguished from another. These major differences which distinguish one race from another have been shown to be hereditary. Is this likewise true of those minor differences which distinguish one individual from another of the same race?

This question can be answered by the well-known method of computing coefficients of parental-filial correlation—the "coefficients of heredity" of Pearson. I realize that the validity of this measure of the force of heredity has been called in question,[17] on the ground that

[17] By Pearl (1911) and Johannsen (1913), among others.

it does nothing more than reveal the presence of genetically different strains in a mixed population. This, however, is exactly what I wish to do in the present case. The fact that within a "pure line," where the phenomena of heredity should be least obscured, this coefficient is said to be zero is entirely irrelevant to the present situation. What we wish to ascertain is the degree to which, for example, long-tailed parents tend to have long-tailed offspring. Whether these differences among the parents are due to "mutations" or "fluctuating variations," whether they are due to single "unit factors" or "multiple factors" or no factors at all, are admittedly matters upon which these coefficients throw no light. Such questions must be decided upon other grounds.[18]

In computing these correlations between parents and offspring, we are restricted to characters which are independent of the absolute size of the individual.[19] Characters which fulfil these requirements fairly well are the *relative* tail length (ratio to body) and the relative width of the tail-stripe (ratio to circumference). My data show that the former is largely, and the latter almost wholly, independent of the size of the mouse.

The coefficients are given in Table VI. I have not thought it worth while to include their probable errors, since the significance of the set as a whole is indicated by the magnitude of most of the figures and by the fact that all but two out of the 24 are positive. The weighted means of these coefficients, combining the four races and two sexes, are: relative tail length, +0.297; tail-stripe,

[18] One objection, valid in certain cases, has been raised against the use of this coefficient. I refer to the contention that it may reveal resemblances which are due not to genetic relationship, but to environmental influences which are similar for parent and offspring, while dissimilar for distinct descent lines. If any one is disposed to raise this objection in the present case, it is sufficient to reply that all of my parent animals of a given race were trapped in the same restricted area, while all the offspring were reared in captivity under conditions which were practically identical for all.

[19] Unless size, itself, were to be taken as the character in question. The absolute length of the tail or foot, on the other hand, is not available for such computations. The progeny of long-tailed parents might have relatively long tails, which might, none the less, be absolutely short, owing to the small size of the individuals in question.

TABLE VI

	rubidus		*gambeli* (La Jolla)		*sonoriensis*	
	Tail	Tail-Stripe	Tail	Tail-Stripe	Tail	Tail-Stripe
Father-son	+0.36	+0.08	+0.15	+0.36	+0.23	+0.26
Father-daughter	+0.24	+0.27	+0.11	+0.53	+0.42	+0.17
Mother-son	+0.64	+0.57	+0.51	+0.36	+0.28	+0.26
Mother-daughter	+0.84	+0.47	−0.02	+0.51	+0.15	−0.02

+ 0.302. The average of four figures given by Pearson[20] (father-son, father-daughter, etc.) for the heredity of stature in man is + 0.335. There is thus found, in these mice, approximately the same degree of resemblance between parents and offspring, in respect to these two characters, as is found to occur in man in respect to stature.[21]

Since the heritability of these individual differences has been proven by means of correlation coefficients, the practicability of selection experiments with such characters is evident, provided that sufficient numbers of normal animals can be reared. Experiments of this nature have already been commenced by Mr. H. H. Collins and myself. The characters chosen for these tests are coat color, tail length and width of tail stripe.

VI. Hybridization

Successful hybrid matings have been made (1) between the Berkeley and the Victorville mice, (2) between the Eureka and the La Jolla mice, and (3) between the Eureka and the Victorville mice.

In the first case, moderate numbers of F_1 and F_2 animals were reared. In respect to coat color, the 25 F_1 individuals, when adult, ranged from a condition similar to that of an average Berkeley *gambeli* to a condition as pale and as yellow as that of the average *sonoriensis*. Moreover, there was here no marked tendency for the mean or intermediate condition to preponderate numerically over the extremes.

20 1900, p. 458.

21 It is likely that the abnormal condition of the cage-born mice, described above, has resulted in minimizing this correlation. Some of the differences among them are doubtless due, not to heredity, but to differences in the incidence of the disturbing factor (infection?). The parents, having grown nearly or quite to maturity in the wild state, were not subjected to this influence.

Now it is of interest to note that the F_2 generation, consisting of 40 specimens, presented very nearly the same range, in respect to coat color, as did the F_1. The two dark extremes were of an almost identical shade, as were likewise the pale extremes.[22] No argument for "segregation" could be based upon this series which would not apply with equal force to the F_1 series.

Twenty F_3 mice, resulting from random matings of the F_2 animals, presented a range of variation which was actually not as great as that observed in the F_2 generation. The smaller number may perhaps be responsible for this difference.

It must be added that both of the parent races present a rather wide range of variability as regards coat color, and that series of the two overlap rather broadly in this respect. This circumstance complicates our interpretations much more in the present case than in that of the crosses between *rubidus* and *sonoriensis,* which will be considered later.

The Berkeley and Victorville races have been found to differ in only two of the characters which were subjected to careful measurement. The former race has a broader dorsal tail-stripe and slightly shorter ears. The second of these differences is a trifling one, however, and is not always evident when small series are compared. Moreover, the absolute length of the ear is largely dependent upon the size of the body.

Thus the width of the tail-stripe is the only accurately measured subspecific character which is available in considering hybrids between these two races. Table VII gives the mean value and the variability of this character in the two parent races[23] and in the F_1 and F_2 generations of hybrids.

Despite the small numbers of animals here concerned, two facts are of some interest. (1) The mean width of the tail-stripe in both generations of hybrids is very

[22] These remarks are based upon a comparison of skins, after death.

[23] The parent mice here used were cage-born animals, which, as before stated, were somewhat modified by captivity. They represent the limited stock which was reared in Berkeley during the earlier stages of the experiment.

nearly midway between the mean widths found in the parent races. (2) There is no increase in the variability

TABLE VII

	Number of Animals Measured	Mean	Standard Deviation
gambeli (Berkeley)	23	33.5	4.09
sonoriensis	38	26.5	4.57
F_1 hybrids	24	30.2	3.96
F_2 hybrids	38	29.3	3.54

of this character in the F_2 generation. Indeed, the standard deviation for the latter animals chances to be the lowest of the four values given.

It seems worth while to indicate the actual distribution frequencies of the tail-stripe measurements for these four groups of mice (Table VIII).

TABLE VIII

	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	Average
Berkeley *gambeli*					1				1	1	1		3	2	3		2	2	4	1	1	1	33.5
sonoriensis	2	2	2	3	2	4	2	2	2	4	3	2	2	1	1	2	2						26.5
F_1 hybrids		1				1		1	3	1	4	2	1	4	1	2	2				1		30.2
F_2 hybrids				1	1	1	3	3	4	2	6	2	3	3	3	4	1	1					29.3

In contrast to this case of the tail-stripe, it is interesting to note that, in respect to relative tail length, the F_2 generation shows a somewhat higher variability than the F_1 generation or than either of the parent races. But it so happens that this is a character *in which the parent races do not appreciably differ.*

In reality, it is probable that none of these differences in variability is significant, in view of the small numbers of individuals concerned. The explanation offered for certain differences between other hybrids to be discussed later—namely, that the F_1 and F_2 generations differed in the relative degree of abnormality—does not seem to apply here. The mean body length is about equal in the two generations, as well as the mean length of tail and foot.

The crosses between the Eureka and the La Jolla races have not been carried far enough to render any report upon them possible at present.

Hybridization of the Eureka with the desert mice was first accomplished nearly two years ago, and thus far 30 F_1 and 20 F_2 animals have been reared to maturity and measured. A very serious drawback has been the great infertility, under local conditions, of *rubidus* and anything having *rubidus* "blood." Still more serious is the abnormal state of a large proportion of the cage-born animals, which affects some of the very parts that we are chiefly concerned with in these crosses. Fortunately, the coat color remains nearly, or quite unaltered.

My series of 30 F_1 skins, taken as a whole, presents a condition about intermediate between that of the parent races. They exhibit, however, a wide range of variation, the darkest individuals being nearly as dark as some of the palest wild specimens of the Eureka race, while the palest individuals differ little in shade from a medium mouse of the desert race (Fig. 13).

In the F_2 generation we meet with a range which is little, if any, greater. The darkest skin[24] is somewhat darker than the darkest in the F_1 generation. On the other hand, the palest skin is scarcely as pale as the palest in the F_1. The preponderating effect is that the hybrids of the second generation, like those of the first, are *intermediates.* If these differences of coat color are conditioned at all by Mendelian "unit factors," there must be more than one pair of allelomorphs concerned. The monohybrid ratio is obviously lacking, and there is no segregation into distinguishable classes. Furthermore, it must be borne in mind that no indirect evidence for segregation can be pointed out in the F_2 generation which is not equally manifested in the F_1.

TABLE IX[24]

	No. of Animals	Body (Mm.)	Tail (Per Cent.)		Foot (Mm.)		Tail-Stripe (Per Cent.)	
		Mean	Mean	S. D.	Mean	S. D.	Mean	S. D.
rubidus (cage-born) ..	61	87.80	98.5		20.82		38.3	
sonoriensis (cage-born)	121	86.48	78.4		19.22		24.7	
F_1 hybrids...........	21	86.43	88.0	4.3	20.09	0.85	31.3	4.0
F_2 hybrids...........	20	84.70	84.3	6.9	19.45	1.12	33.6	6.5

[24] This happens to be a badly shrunken skin, which perhaps does not reveal the original color. The next darkest (shown in the photograph) is of almost exactly the same shade as the darkest F_1 skin.

FIG. 13. Skins of pale, intermediate and dark individuals of *P. m. rubidus* (first line), of *P. m. sonoriensis* (second line), and of F_1 and F_2 hybrids between these races (third and fourth lines).

As regards the measurable characters which differentiate the parent races, some light upon their behavior in hybridization may be derived from the data in Table IX. Here, too, one fact seems plain, despite the small number of individuals, and the modifications which these mice share with cage-born mice in general. This is the intermediate condition of the hybrids, both F_1 and F_2, as regards tail length, foot length and tail-stripe. The ear measurements have not been introduced into these comparisons, since the parent races do not differ in this respect.

As regards variability, it is seen that the standard deviations of the F_2 generation are all three larger than those of the F_1, and the differences seem great enough to be of possible statistical significance. I have, however, tabulated the frequencies of the various values for these three characters (not reproduced here), and I find that the probable explanation of this increase of variability in the F_2 generation is an increase in the amount of abnormality in the latter. This is to be inferred from the fact that the extension in range is chiefly in the direction of the *lower* values, while in two of the three cases the uppermost figures actually fall below those of the F_1. Now the abnormal influences of captivity operate by decreasing (oftentimes considerably) the values for these very characters. As further evidence for this interpretation is the fact that the average body size of the F_2 mice is here less than that of the preceding generation.

A considerable number of back crosses have been obtained between each of the hybrid combinations above discussed and one or both of the parent races. The number of individuals in any one series is, however, small, so that it is hardly worth while to deal with the results of these crosses here. They afford as little evidence of complete segregation of the subspecific color types as do the hybrids previously considered.

(*To be concluded*)

[25] Standard deviations for the parent races have been computed only for the two sexes separately. They are, therefore, not included in this table. Nine of the 30 F_1 animals are not here included, since the *rubidus* parents of these were caught at some distance from Eureka.

INTERNAL FACTORS INFLUENCING EGG PRODUCTION IN THE RHODE ISLAND RED BREED OF DOMESTIC FOWL. III

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Winter Egg Production and the Genetic Constitution of Rhode Island Reds.—Pearl, '12, found his Barred Plymouth Rocks fell into three well-defined classes in regard to winter egg production, viz., those that did not lay at all before March 1, the zero class; those that laid less than thirty eggs with a mean at about 16 eggs, the mediocre producers; and finally those that laid over thirty eggs, the high producers. Pearl has stated, however, that the existence of the two classes of birds, mediocre and high, is the important point rather than the number of eggs at which the dividing line falls, which may be below 30 eggs in some flocks and above 30 in others. Since the record of No. 5080 is that of a typical true mediocre producer; it is clear why the division point need not fall at a particular number of eggs. If, however, the numerical record of a pullet is made the only basis for a division point, it may be pointed out that the point could be shifted by differences in environment. If, on the other hand, under the same general environment one flock was found to have a different point of division from the second flock, the latter could not be considered genetically like the first. Thus far, no satisfactory division point has been found for our Rhode Island Reds, due probably to the few records of the type shown by No. 5080 (that is, to an absence of true mediocre producers) and to the great variability in age at first egg, associated with a comparatively uniform rate of production after

the appearance of the first egg. While a true mediocre producer such as No. 5080 can easily be distinguished from a high producer in Barred Plymouth Rocks, it is impossible to draw a division line on the basis of the number of eggs produced where the egg production is of the sort observed in our Rhode Island Reds. (See Figs. 3 and 4.) Except in the case of a few individuals, the only evidence for the existence of two genetically distinct groups, such as Pearl found for Barred Plymouth Rocks, is in the shape of the left-hand portion of the curves of winter egg production. If the zero producers be omitted as a wholly artificial group (*cf.* Figs. 8 and 17) this evidence becomes less satisfactory, especially as the excess of numbers on this side of the curve may well be due to environmental factors, since the effect of such factors is almost always in the direction of decreased production. Moreover, in a later paragraph it is shown that the shape of these curves depends upon certain clearly recognized factors.

In order to eliminate any miscomprehension in regard to the characteristics of a mediocre producer, I have gone over the matter personally with Pearl. It appears that his Barred Plymouth Rocks, with the exception, of course, of the zero producers, begin to lay at about the same age, but lay at *widely differing rates.* My Rhode Island Reds, on the contrary, begin to lay at widely different ages, but lay at a fairly *uniform rate.* In the Barred Plymouth Rocks, therefore, there are three distinct *types* of winter records, zero producers, mediocre producers (Fig. 12, Nos. 274 and 284) and high producers (Fig. 3). The same types of records have appeared in a flock of Brown Leghorns which we have trap-nested.

In our Rhode Island Reds, records of the mediocre type are so rare that they must be referred either to some non-genetic origin, or a chance union of two heterozygotes, such as results in the appearance of an occasional recessive in a flock that characteristically has some domi-

nant character such as rose comb. It is quite possible that while our flock of Rhode Island Reds as a whole is homozygous for high fecundity, it is not entirely so. It is possible, of course, that many of our Rhode Island Reds are genetically true mediocre producers, but that the addition of some other genetic factor has so altered the rate of production that the records can no longer be recognized as true mediocre records.

It seems clear, then, that our Rhode Island Reds fall into the class of high producers observed in Barred Plymouth Rocks, but that the great variability in maturity results in a portion of the flock giving numerical results like those of the Barred Plymouth Rocks, but which in reality are not at all equivalent biologically. It is also clear why Castle's ('15, '16) recent criticism of Pearl's theory of egg production can not be considered to be established, in so far as it concerns *winter egg production.*

Moreover, it will be desirable in the future to distinguish clearly between the two sorts of numerical results. A discussion of the bearing of a division point at 30 eggs upon the problem is given below.

It has been maintained by Pearl that winter egg production is a satisfactory basis for selection, both for itself and as an index of the annual egg production. This would be true only when there is a definite relation between winter and annual production such as he has found for Barred Plymouth Rocks. Since winter egg production forms a part of the annual egg production with which it is to be compared, it is evident that the coefficient of correlation may be expected to have a positive value of some magnitude, unless there is a definite tendency for birds that lay well in the winter to be poor layers in the summer. On this account it has seemed best to us to compare winter production with that of the same hens for the remainder of the year. The number of birds (77) available for the comparison was not large; but the calculated coefficient ($.365 \pm .067$), while statistically significant, being six times its probable error, is too small

for use in breeding operations. While there is an evident tendency for a high winter producer to be also a high producer for the rest of the year, it seems also true, as far as the 1913–14 records are concerned—those of 1915 being at this writing incompletely worked out, though of the same general order—that there is no special tendency for birds of late start to stop early rather than late. Of course it is essential that a bird lay well in the winter if she is to make a good yearly record, and in this sense the winter egg production may be of value as a measure of fecundity, but good winter production does not insure a good annual production, nor does a low winter production necessarily mean a poor annual production. It is true, however, that birds that make the very highest records must lay throughout the entire year. From the data in hand it seems probable that winter egg production of Rhode Island Reds is not as valuable a measure of the innate fecundity capacity of a bird as it is for the Barred Plymouth Rocks.

On the average, the flocks, if grouped according to the month hatched, have an annual record that differs by an amount equal to an average winter month's production, viz., 10 eggs, as shown by Table VIII. Or, to put the matter a little differently, the average egg production of pullets hatched in March, April or May is approximately the same from February 1 to November 1. We have no evidence that the early hatched birds, on the average, stop laying earlier in the fall than those hatched later.

The influence of time of hatching on a division point at thirty eggs is very marked in the Rhode Island Reds. In Table VI the egg production of pullets laying at all during the winter is divided into an over-thirty and an under-thirty class. In the former are 68.8 per cent. of the March-hatched pullets, 58.7 per cent. of the April-hatched pullets, while of the May-hatched birds there are only 26.6 per cent. The means of the over-thirty class are 63 eggs for the February-hatched pullets, 54.9 for the March, 46.3 for the April birds, while that for the May

TABLE VIII

EGG PRODUCTION OF PULLETS HATCHED IN APRIL, MAY AND JUNE, 1915; SHOWING NUMBER OF EGGS LAID PRIOR TO AND AFTER MARCH 1, ALSO PRIOR TO AND AFTER FEBRUARY 1

	Months Hatched		
	March	April	May
Number of pullets	139	140	116
Total eggs before March 1	5,780	4,470	2,253
Total eggs after March 1 to end of year	12,951	12,974	10,982
Av. number of eggs before March 1	41.6	31.9	19.4
Av. number of eggs after March 1	93.2	92.8	94.6
Grand total	18,731	17,444	13,235
Av. yearly production	134.8	124.7	114.0
Av. number of eggs for February	10.3	12.0	11.9
Av. number of eggs before February 1	31.3	19.9	7.5
Av. number of eggs after February 1 to end of year	103.5	104.8	106.5

Note.—The data above the double bar is for birds that completed the year. A part of the data below the double bar was compiled at the end of the winter and thus includes some birds that died during the summer.

birds is 40.5. The means of the under-thirty class are 18.8 for February and for the other three months approximately 16 eggs. Now, the mean for the abstract numbers 1 to 30 is 15.5, a value which is not far from the observed mean, since the value of 18.8 eggs obtained for the February birds is probably due to the small number of individuals involved. As the value of the mean for the under-thirty birds is practically alike in all cases, and as the value of the means for the over-thirty class for the various months decreases with decreasing age, it is evident that the value, 16.1, comes mainly from the relation of the abstract numbers and has little or no significance in itself. This point will be returned to shortly.

It will be noted in Table VI that the percentage of over-thirty pullets dropped very suddenly in passing from April to May. It means, I take it, that many of the May-hatched birds did not reach a winter egg production of 30 eggs or over because of the time they were hatched. Indeed, something of this sort is to be expected when a definite number of eggs is taken for a dividing line at a particular point on the calendar. If the production curve

for May-hatched pullets be examined it will be noticed that there is a large percentage of pullets in the 16–20, 21–25, and 26–30 groups. If the average monthly production of about 10 eggs be added to these groups, most of them become over-thirty birds and the percentage of over-thirty birds becomes nearly the same as that for the April-hatched pullets. This is important, since it indicates that May-hatched Rhode Island Red pullets mature too late to furnish data comparable to Pearl's Barred Plymouth Rocks, for which it is stated (Pearl '15) that April- and May-hatched pullets alone give normal records.

Birds that begin to lay by January 1 and lay at the rate of 15 eggs per month would lay 30 eggs before March 1. This rate is about the lowest *continuous* production that has been noted, for birds that lay at a less rate usually lay intermittently. Pullets that lay at the rate specified and which begin sufficiently early in the season make very good winter records. In a recent paper Pearl, '15*b*, has remarked:

> Any bird laying 18 or more eggs per month in the months of November, December, January and February may certainly be regarded as a high winter producer.

The statement as written might imply that this rate is maintained throughout all four months, but, as this means 72 eggs and as the context implies, we take Pearl's statement to mean 18 eggs for any one month. At this rate a bird beginning to lay January 1 would lay 36 eggs before March 1. Since, however, the mode of the frequency curve of age at first egg falls at the 251–260 days group, and since the median also falls near this group, it means that nearly one half of a flock of pullets hatched May 1 will not begin to lay till after January 15, and therefore will lay less than 30 eggs. The slope of the curve indicates, moreover, that the upper limit of the range falls at about 311–320 days, which means that a few individuals begin to lay so late in life that they can not be expected to make normal records. Ten months from hatching time brings birds hatched the last of April into laying some

time in February. Three hundred and ten days seems, moreover, to mark the approximate boundary of a group of stragglers which perhaps corresponds to Pearl's after March 1 group of producers, *i. e.*, his zero producers. This group is represented in the curve by the shoulder which begins at this point, there being of course an overlap with the larger group, beginning somewhere about 280–290 days.

The relation of the *abstract* numbers involved in the series of data relating to winter egg production is a matter of some importance. The mean of the abstract numbers from 1–30 is 15.5, or from 0–30, 15, a value that corresponds closely to the mean value of the number of eggs laid by the under-thirty class. The mean value of the numbers above 30 beginning at 31 and proceeding to some other higher number such as 50 or 80, will depend in part on the value chosen for the higher number. If 80 be chosen as the higher limiting value, then the mean of the numbers 31–80 is found to have a value of 56.2. The mean values just given hold only when the abstract numbers are taken one at a time or when they are arranged in a symmetrical fashion about the mean, as, for example, in the ratio of 1:2:3:4, etc., and back to 4:3:2:1. If the 1–30 winter egg production group represented a definite genotype one would expect a symmetrical or nearly symmetrical distribution of the concrete numbers about their mean. If, however, the numbers (abstract or concrete, as the case may be) had some other sort of arrangement—as, for example, if they formed part of a normal curve of variation—a different set of mean values would be obtained, depending upon the steepness of the slope of the curve. If, for example, the classes 1–5, etc., to 25–30 inclusive, are formed and the central values appear in the ratio of 1:1.3:1.7:2:2.3:2.7, the mean will be 18.2. On the other hand, the mean of the abstract numbers above 30 that form the remainder of the normal curve, under some circumstances may shift downwards, as, for example, when the mode of the curve is at 50 with the

upper limit of the range at 90. If the observed distribution of winter egg production is mono-modal, and if its curve, base, mode and range correspond approximately to those of the curve assumed in the preceding paragraph, the mean of the numbers 1–30 will be larger than the mean (15.5) obtained from the abstract numbers in the manner chosen at the beginning of the paragraph. That is, there is a tendency for the means of the two parts of the mono-modal curve, *i. e.*, the ones derived from 1–30 and 30–90, respectively, to approach each other in value. If, however, the curve of winter egg production is a composite of two curves, *i. e.*, mediocre and high producers, then the means tend to approach those of the abstract numbers involved when distributed symmetrically.

Some doubt exists as to how our data are to be interpreted in the light of the statements in the preceding paragraph. The mean of the under-thirty group—viz., 16—while slightly higher than that of the mean for the abstract numbers—viz., 15.5—probably is not significant, though it may perhaps be taken as an indication of the existence of two genotypes. Since, however, the mean of the over-thirty group increases with increasing age and since the percentage of birds falling in the over-thirty classes increases with increasing age, it seems probable that the shape of the observed egg production curves is due to the artificial division point at March 1, while the irregularities in the curves are due to too few numbers. Since these irregularities largely disappear if the class intervals are doubled and since, if the time limits were to be extended so as to permit all birds to begin laying, it appears probable that the curve would become a symmetrical unimodal curve. Moreover, this conclusion is strengthened by the fact that the observed mean, 46.3, of the over-thirty class of the April-hatched pullets with its upper range at 77 is lower than the value (56.2) noted for the abstract numbers 31–80. For Barred Plymouth Rocks, however, the means do not rest upon the relation between the abstract numbers, but are an expression of the average production of the two types.

A comparison of the winter egg production curves obtained with the Rhode Island Reds with the similar curves for various seasons for the Barred Plymouth Rocks

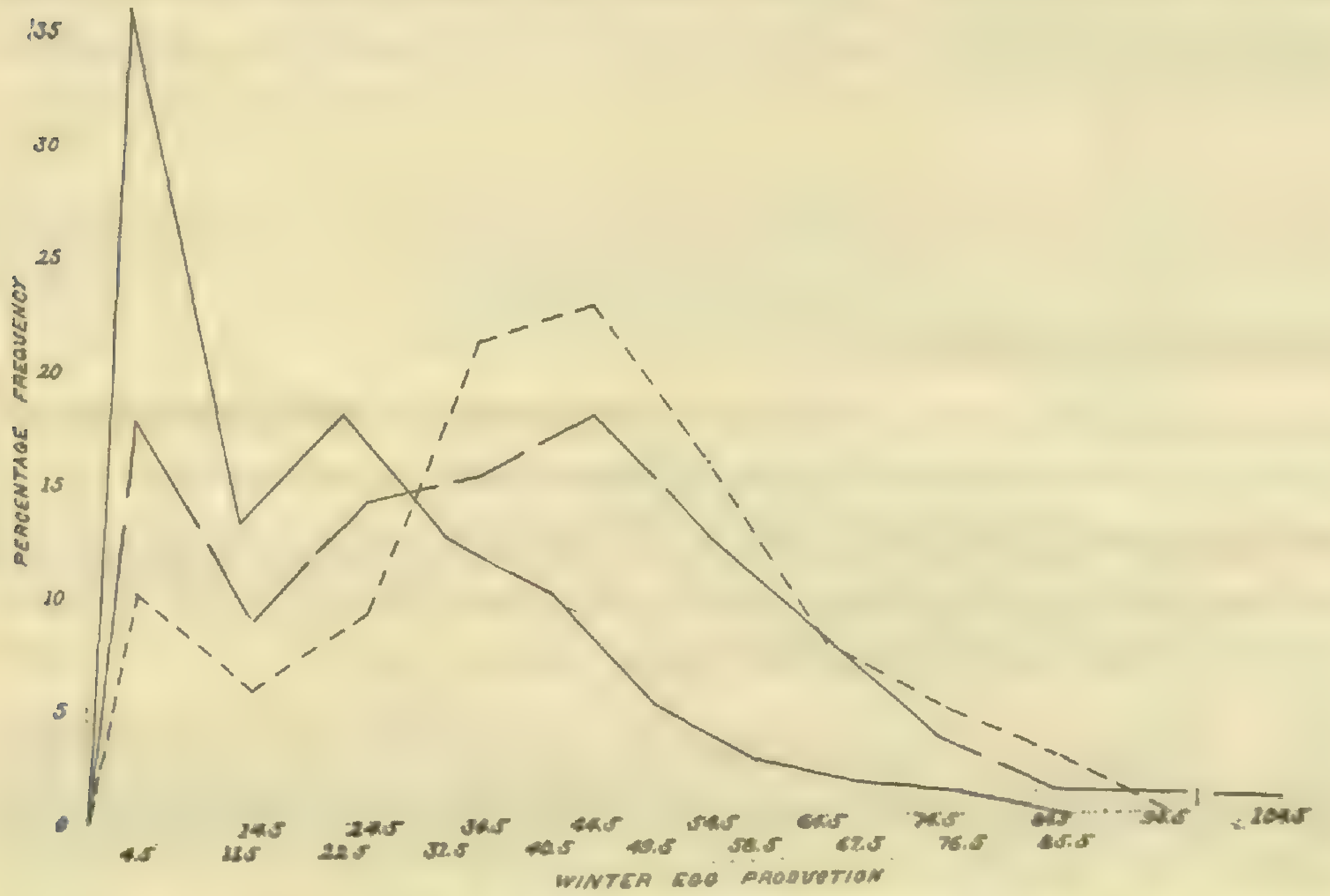

FIG. 14. Comparison of a flock of Barred Plymouth Rock pullets (Maine. 1907–08, solid line) with two flocks of Rhode Island Red pullets (Mass., 1915–16, broken line; Mass., 1913–14, dotted line) to show the difference in the shape of the winter egg production curves. For the present purpose it seemed unnecessary to regroup our data to correspond exactly to the Maine Station grouping.

brings out some interesting points. These curves are shown in Figs. 14, 15, 16 and 17. In Fig. 14 the continuous line is the frequency curve for the winter egg pro-

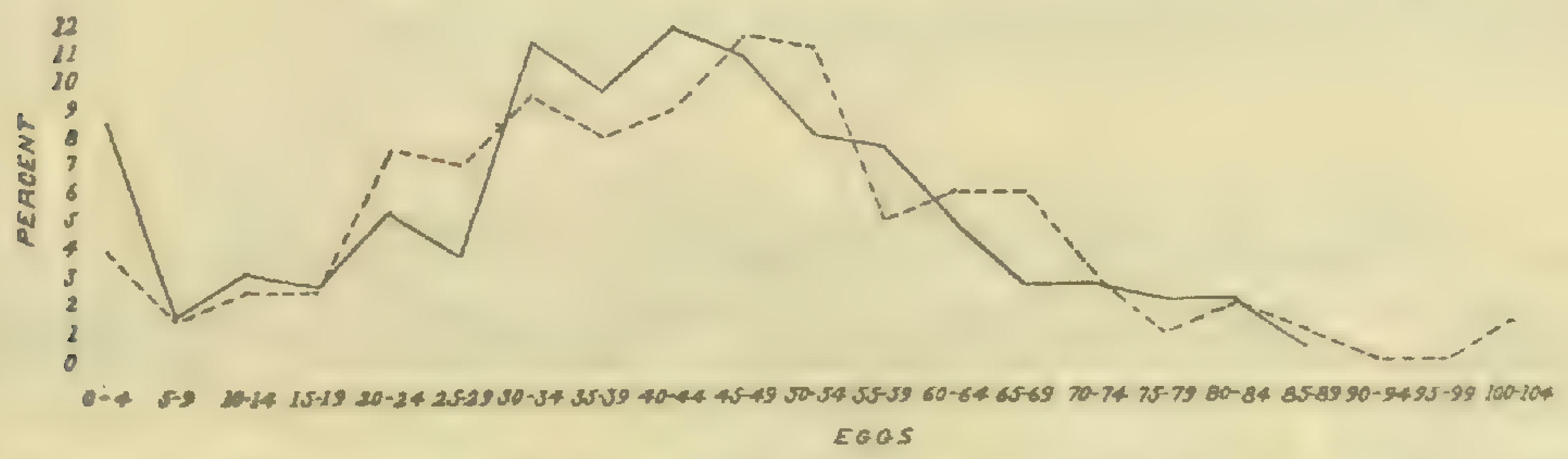

FIG. 15. Comparison of a flock of Barred Plymouth Rock pullets (Maine, 1912–13, dotted line) with a flock of Rhode Island Red pullets (Mass., 1913–14, solid line) to show the similarity in the distribution of winter egg production.

duction at the Maine Station for 1907–08, the flock reared by Pearl from the birds previously bred by Gowell for increased egg production. The line composed of short

dashes is the curve of egg production for the winter of 1913–14, made by our Rhode Island Reds hatched in March and April. This flock is the first flock about which we have full data. They were the daughters of the original flock, 1912–13, as described above, and for all essen-

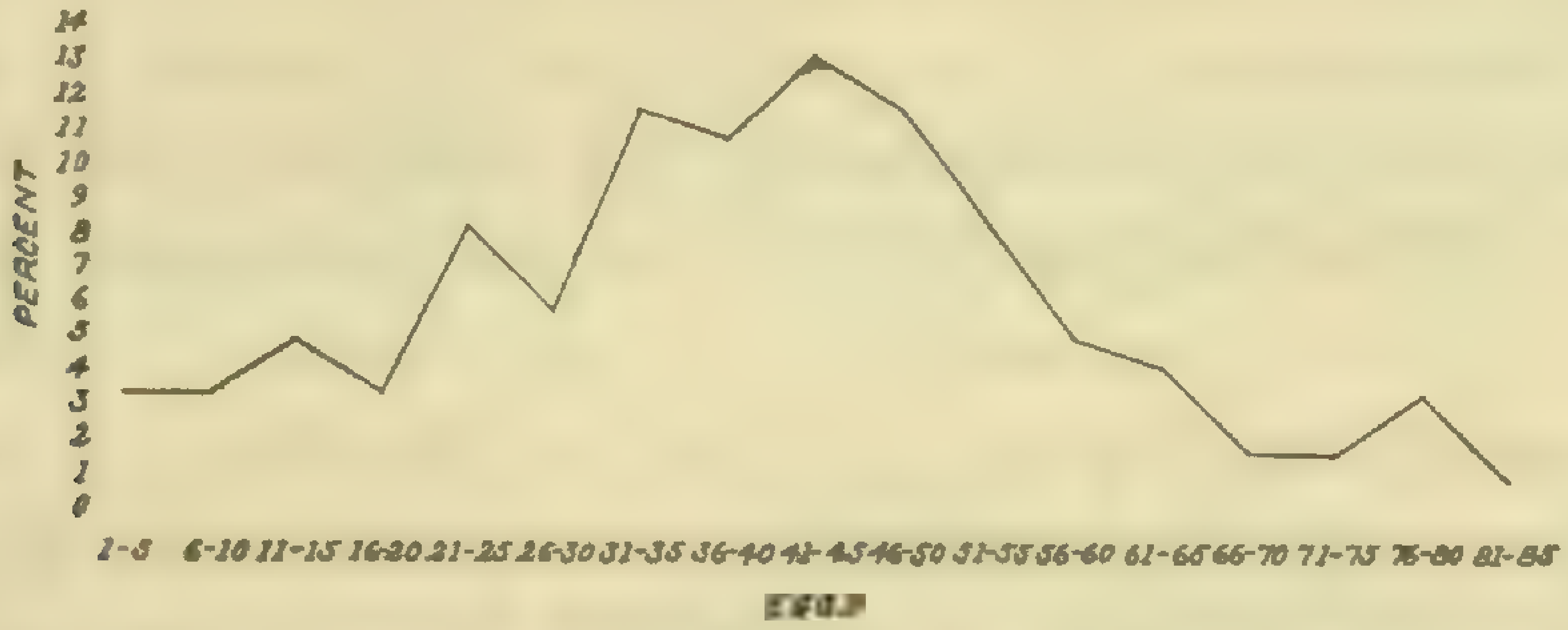

FIG. 16. Winter egg production of the Rhode Island Red pullets hatched in April, 1913. The records of these pullets have been separated from the records shown in Fig. 14 (solid line).

tial purposes were a random selection of individuals. This flock, one generation removed from its standard-bred ancestry, clearly differs from the 1907–08 flock of Pearl's in containing many more fairly high birds. The data for the 1913–14 flock, grouped in classes of 1–5 instead of 1–10,

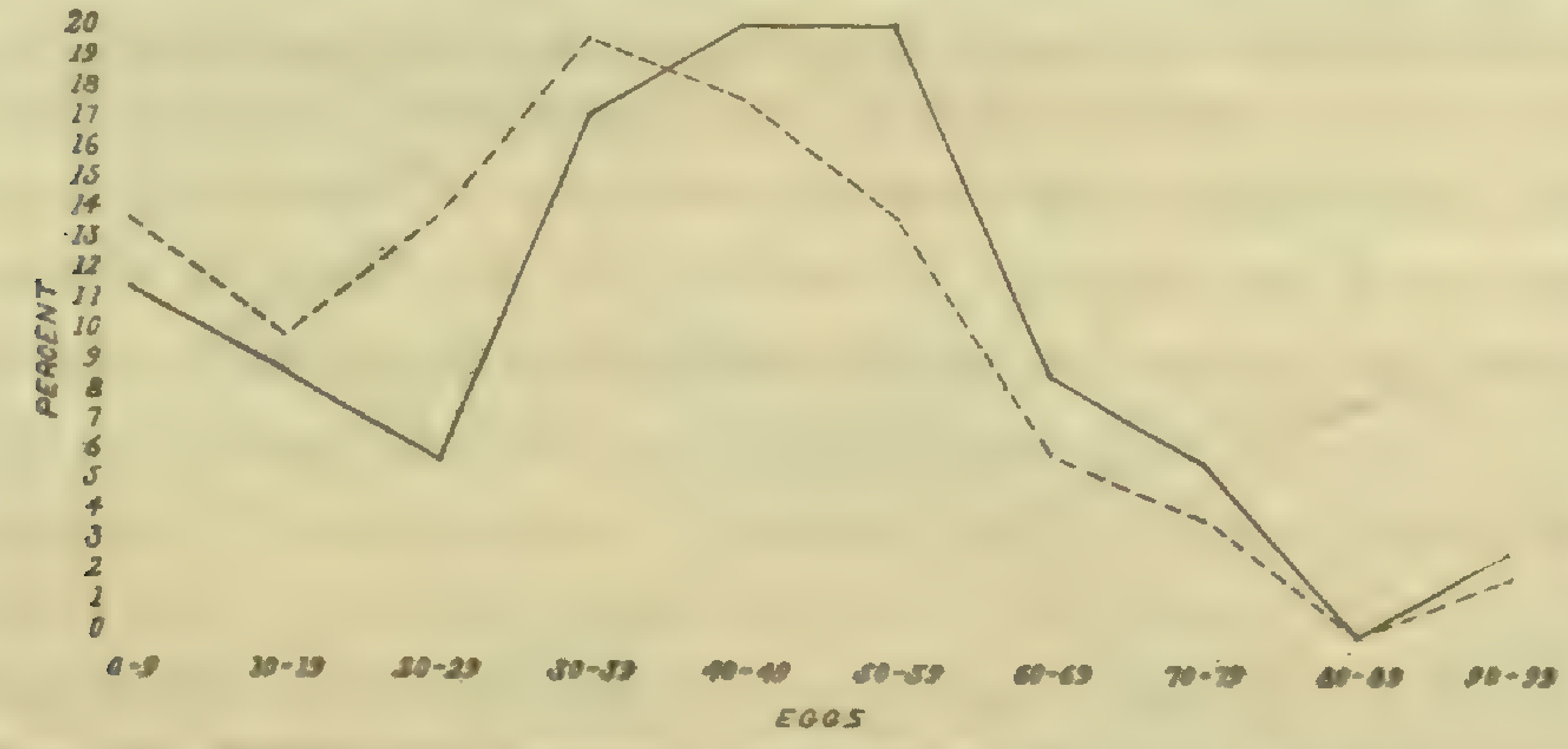

FIG. 17. Winter egg production of the flock of pullets reared in 1916 from eggs purchased of the breeder furnishing our foundation stock. The solid line represents the March hatched pullets; the broken line, the March pullets plus April hatched pullets from the same source.

is shown by the continuous line in Fig. 15, where it is to be compared with the winter record of 199 Barred Plymouth Rocks made at the Maine Station for 1912–13.[6] The essential similarity of the two curves is self-evident. As

[6] The data for the Barred Rocks was taken from Pearl (15*c*).

Pearl's pullets were (presumably) hatched in April and May, while ours were hatched in March and April, the curve for the April, 1913, hatched pullets alone is given in Fig. 16, which shows that the separation of the March pullets from the April pullets has not essentially altered the shape of the curve. The zero producers were omitted in order to study the shape of the curve when treating the zeros as an artificial group. This omission, however, would not alter the essential shape of the curve.

As already stated, new blood was added to our breeding pens in 1915. The egg production curve made by the pullets hatched in March and April for 1915–16 is shown by the broken line in Fig. 14. Compare also the separate curves for March- and April-hatched pullets shown in Fig. 8. Although some individual records better than any previously obtained were secured, on the whole egg production was not as good as for 1913–14, although still distinctly better than the production of the 1907–08 flock of Barred Plymouth Rocks.

The figures when grouped according to the month in which the birds were hatched show clearly the part played by this factor in determining the sort of records made. The curve for the March-hatched pullets is quite similar in appearance to the curve made by Pearl's Barred Rocks in 1913–14, except that the mode falls at a lower number of eggs. That is, the Barred Rocks contained a higher percentage of birds laying above 50 eggs than the March-hatched Rhode Island Reds. The curve, however, for the May-hatched Rhode Island Reds is much more like that of the 1907–08 curve of Barred Plymouth Rocks, while the curve for the April-hatched pullets is intermediate between the two.

It seemed a matter of some interest to determine whether our 1913–14 record was a chance record or whether it was a fair sample of the original stock. Consequently eggs were purchased from the original source and chicks reared in 1915. The first lot was hatched March 22 and all the pullets (39) that passed the test for

vigor were put into a laying house in October. The egg-production curve is shown by the continuous line in Fig. 17. It bears a strong resemblance to that of the Maine Station for 1912–13 and that of our flock for 1913–14. There was in addition to the 39 pullets a smaller lot hatched April 27. The curve for both lots combined is shown by the dotted line in Fig. 17. Again the curve is essentially like the 1913–14 curve for Rhode Island Reds. The writer would be glad to study the original stock in more adequate fashion, but the amount of time, labor and equipment required are so great that the end in view did not seem to warrant the expense.

Since Pearl has not discussed the question of age at first egg from the present standpoint, the possibility must not be overlooked that the factor of maturity may play an important part in his results. In a recent paper (Pearl, '16) he states that in a good laying strain the pullets mature at five or six months on the average. Quite a different state of affairs exists in our Rhode Island Reds, where the average age is much higher, about 8½ months for the entire flock. It is clear, however, from the discussion that the factor of maturity does not influence his results to any considerable extent.

Since the two principal internal factors responsible in most cases for the number of eggs produced by a pullet during the winter are, first, the date of the first egg, and second, rate, similar sets of data may result from variability in either of the two factors. Now the date of the first egg is dependent in part on the time of year the bird is hatched, and in part on differences in maturity. The former factor is under control and can be used to eliminate differences in maturity. Rate has already been discussed in another place, but it should be noted that it may be modified by such definite factors as broodiness, or the presence or absence of cycles, as well as other physiological factors that appear to be innate but which can not be named at present. The combined effect of rate and date of first egg, or better the length of time

elapsing between the first egg and March 1, is such that the same number of eggs may result from a variation in either one of these factors. If a flock of birds all begin to lay about the same time of year, but vary greatly in the rate at which they lay, a body of data superficially the same as that produced by a flock of birds laying at a fairly uniform rate but varying greatly in the time at which they begin to lay might readily result, especially if the variability of each set of factors (rate or maturity) was very much alike. Radically different sets of data would result only if the variability belonged to quite different types. The birds that make *unusually* high winter records are those that start early and lay at a good rate throughout the winter. A poor record, on the other hand, results either from a low rate combined with a long period of production (the date of first egg coming early in the fall) or from high rate and a short period of production, since the date of first egg comes late in the winter.

A late date of beginning egg production may be the result of late hatching or of delayed maturity. That is, an early-maturing bird if hatched too late may lay no more eggs than a late-maturing bird hatched early in the spring. Thus, the actual record of a bird is the result of the influence of several factors, themselves very variable, and gives much the same result as though a much larger number of factors were involved.

Pearl has spoken of two production factors, L_1 and L_2, but has not, so far as I know, assigned either to the two chief factors concerned in winter egg production, viz., rate and age at first egg, nor does the context indicate any such sense. At first sight it might seem possible that one of these factors is a factor for early maturity, the other for rate; for according to Pearl's theory both factors must be present to secure high production, since the L_1 factor in the homozygous condition does not make a high producer. So far as can be seen, there is no objection to assigning one of Pearl's two factors to rate. Some difficulties are encountered, however, in assigning maturity

to either of Pearl's factors, for early-maturing birds almost invariably lay more than the required number of eggs even when their production is interrupted in some way. Since, however, the theory demands that both genetic factors be present for high production, the assignment of one factor to rate and the other to maturity can not be made.

THE SHAPE OF WINTER EGG PRODUCTION CURVES

The curves of winter egg production are clearly compound curves, probably belonging to the "S" type described by Pearl and Surface for monthly egg production in Barred Plymouth Rocks.

In the case of the winter egg production curves, it can be shown that this type of curve is due primarily to the variability in age at first egg, plus the date at which the census of the flock is taken. The curve, however, is modified somewhat by the variability in rate and by the fact that the birds were not all hatched at the same time. If a flock of birds were all hatched on the same day and all laid at some uniform rate, say an egg per day, it is clear that, on any given date between the date the first pullet commenced to lay and the date the last one began, the frequency polygon showing the number of eggs produced would consist of a zero class plus the remaining portion of the polygon, beginning at class 1 and proceeding through classes 2, 3, 4, etc., to the upper end of the range. Now the number of birds laying one egg apiece would depend upon the date chosen for the census and would be the number of birds that reached a given age on that date as shown by the curve of age at first egg. Thus, if Fig. 1 be taken as our standard, and some date early in the season be chosen for the census, say the date on which the flock becomes 186 days of age, the zero component of the egg curve would have a value of 99 per cent. and the 1-egg class a value of .6 per cent. At mid-season (256 days) the zero component would have an ordinal value of 55.3 per cent. and the 1-egg class a value

of 14.3 per cent., the 11-egg class a value of 9 per cent., the 21-egg class a value of 11.4 and so on. Towards the end of the season, say at 306 days, the value of the zero class would be 13.3 per cent., and the 1-egg class would have a value of 3.1 per cent., the 11-egg class a value of 5.1 per cent., the 51-egg class a value of 14.3 and so on. At the close of the season, 366 days, the zero class disappears, while each egg class has the percentage values given in Fig. 1, beginning at the extreme right and proceeding to the left, *i. e.*, the egg curve is a mirror image of the age at first egg curve.

The first modifying factor, *i. e.*, rate, tends to flatten the theoretical egg curve by shifting individuals from one side toward the other. Thus, an individual falling in the 56 class, on the 100 per cent. rate, would fall into the 36 class at a 66⅔ rate. If a 50 per cent. rate were selected as the theoretical rate, the 66⅔ rate hen would be shoved over into the 76 class. If the date of the first egg of a sufficiently large number of pullets all hatched on the same day were plotted on a suitable calendar, a duplicate of the age at first egg curve would be obtained; but if several hatches are grouped together, *e. g.*, the four hatches occurring in any one month, it is evident that the curve plotted on the calendar would be considerably flattened and in turn would flatten out the theoretical curve of egg production as based on age at first egg.

Selection.—Pearl's success in securing increased egg production by breeding might be due to his methods of selecting the breeders, regardless of all theoretical considerations. Families that contained all high producers were selected generation after generation to propagate the high fecundity lines. Families in which true mediocre producers appeared, *i. e.*, where segregation took place, were not used in breeding for *increased* egg production. This type of selection could hardly fail to yield results, provided that egg production is inherited. Nevertheless, it is clear that fecundity is inherited in Mendelian fashion

in Pearl's Barred Plymouth Rocks. However, the results obtained by Dryden at the Oregon Station show that individual selection in pedigreed lines as opposed to mass selection may result in improved egg production quite as well as by the application of Pearl's theory.

Egg production in the domestic fowl may seem at first sight to be a highly desirable character on which to study the influence of selection. It may be regarded as a unit character if one so desires, and if, by selection, this character is changed, it is clear that selection has been effective. But it is also clear that the effectiveness of such selection in this instance rests, in large measure, at least, upon the influence exerted by various modifying factors, such as broodiness or age at first egg, discussed in this paper. It is possible to study these factors individually both by themselves and also in their relation to egg production. Broodiness is known to behave like a Mendelian dominant, while Pearl has shown that the rate of production during the winter cycle is dependent on two genes, one sex-linked, the other a simple Mendelian character. We have found some evidence that the presence or absence of a winter cycle in fowls that lay at all during the winter[7] follows the Mendelian scheme. Since the influence of the various modifying factors is so clear cut, it is evident that egg production is a character wholly unsuited for studying the possibility of the modification of the germinal representatives of a character by selection. On the other hand, it is a good example of a character that varies continuously, but the continuity of whose variability can be shown to depend upon several modifying factors.

There is a point of some general interest regarding the genetic composition of any given flock. Hardy ('08) showed that the proportions in which a Mendelian character occurs tend to remain constant provided no selection is practised. Fanciers often practise a certain but

[7] The absence of a winter cycle in this instance means continuous production throughout the winter and spring, and *not* absence of egg production as in Pearl's Barred Plymouth Rocks.

indefinite amount of inbreeding. Under such circumstances there would be a tendency for the fecundity factors to remain in about the proportions in which they started. We may, therefore, expect to find ready-made flocks of high producers, true mediocre producers, or even zero producers as well as those containing the several types. Thus, the original Barred Plymouth Rocks of the Maine Station contained all three types, while the Cornish contain only true mediocre and zero producers.

In spite of the fact that we have *as yet* been unable to apply Pearl's theory of egg production bodily to our Rhode Island Reds (although it may yet be possible to use it after making some modifications) there is no question but that the ability to lay is inherited, as shown by a better egg production in some families than in others. It is clear also that some males produce offspring that on the whole make much better records than those from other males when the two groups of females with which they are mated are very similar in their winter egg production. In one instance, the difference between two sets of offspring by two males was clearly due to a difference in maturity. It seems clear, moreover, that some of the internal factors, such as broodiness and maturity, segregate independently.

Summary

1. The object of the present paper is to present a sur vey of the problem of egg production based on the results of four years' study of egg production in Rhode Island Reds. The presentation of the data is incidental to this object.

2. On account of disturbing factors, data from two years only is presented.

3. There are two main conclusions: First: egg production in our strain of Rhode Island Reds differs in several important respects from Pearl's strain of Barred Plymouth Rocks and also from Leghorns. Second: the egg record of a hen by itself is an unsafe basis on which

to breed for definite degrees of production, for it can be shown that egg production depends on several more or less independent internal factors and that the same number of eggs may result from the action of different sets of factors. It follows, therefore, that each factor must be studied separately, both from the physiological and genetic standpoints.

4. The factors reviewed are: date of first egg, age at first egg, growth, rhythm and rate of production, including here Pearl's genetic factors L_1 and L_2, broodiness, moult, cycles, persistence of production in the autumn, and stamina.

5. Date of first egg is shown to depend on the time of hatching, the rate of growth of the young birds and some elements, at present unknown, that determine the attainment of sexual maturity. On the average it has been found that those individuals that lay early in the fall (October) lay more winter eggs than those that begin to lay later.

6. On the average, pullets that lay relatively early (6 to 7 months) in life lay more eggs than those that lay at a later period (8, 9, or more months) in life, other things being equal. The variability in age at first egg appears to be much greater for our Rhode Island Reds than for Pearl's Barred Plymouth Rocks.

7. Birds that lay rapidly, other things being equal, lay more eggs than those that lay more slowly.

8. Some birds (true mediocre producers) lay very slowly and irregularly, producing only a few eggs (1–10 or thereabouts) per month. Others (true high producers) lay much better (15–28 eggs per month).

9. The effect of the age at which the first egg is produced on winter egg production is such that numerical results, similar to those given by true mediocre producers, may result.

10. Some pullets lay continuously or nearly so, for long periods of time. Others lay relatively rapidly, but lay in cycles with a period of rest in between. These rest

periods may or may not be associated with broodiness. In a large percentage of Rhode Island Reds, a winter cycle comparable to that found in Barred Plymouth Rocks, is absent.

11. Broodiness operates to reduce egg production very materially, for the average production is about 40 per cent. higher for the period prior to the time each individual goes broody compared with average production after that time. The apparent paradox that hens with the greatest number of broody periods lay more eggs than those with fewer broody periods is due to the fact that increased production affords opportunity for more broody periods. The presence of a large amount of broodiness in our Rhode Island Reds differentiates them from the Leghorns, which lack this characteristic.

12. The appearance of a moult often stops production. A partial summer moult was noted.

13. Other things being equal, birds that lay late in the fall lay more than those that stop early.

14. Small birds mature earlier, on the average, than large ones and hence lay more winter eggs.

15. It was observed that while birds of poor stamina might make exceptionally good records, that lack of stamina tended to delay the appearance of the first egg and hence lowered the winter records.

16. It is pointed out that while the results obtained in Rhode Island Reds differ from those obtained by Pearl in Barred Plymouth Rocks in egg production, this difference must be looked upon as a real difference just as the two races differ in color.

17. Egg production is an unsatisfactory character on which to study the possible effects of selection in modifying the germ plasm, because in reality it is complex and not a simple unit character.

18. The genetic constitution of our Rhode Island Reds in respect to Pearl's L_1 and L_2 factors has not certainly been made out, but it seems probable that as a strain they fall into Pearl's class of high producers. True mediocre producers are very uncommon in this strain.

19. The relation between the means of the abstract numbers, in the series 1–30 and 30 to some higher number, and its bearing on the use of the means of egg production of two groups falling within the same limits is discussed.

20. The curves of winter egg production are shown to be compound curves.

21. A knowledge of the factors described is of importance both from the commercial and biological standpoints. As Pearl and Surface ('08) pointed out a number of years ago, the income received from each bird will depend not only on the number of eggs produced, but also on the season at which those eggs are laid. A bird that produces 100 eggs at suitable seasons may yield as much income as a bird that produces 200 eggs at less profitable seasons.

From the biological standpoint, a knowledge of the separate factors is important because what might seem at first sight to be a simple character is really extremely complex. Obviously, then, it is necessary to attack the problem from this standpoint.

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AN EXAMINATION OF THE POLICY OF RE-STOCKING THE INLAND WATERS WITH FISH[1]

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The large sums of money annually expended by both the National Government and the several states in fish propagation fall into two general fields of activity, the marine and the freshwater. The freshwater activity in turn may for convenience be divided into the production of food and game fish.

It is always proper to examine the conditions which influence restocking; and just at this time it is especially fitting to enquire into the efficacy of the methods. The technique involved in securing the eggs and their care during hatching have been well worked out. It was a marked step in advance when these modern methods were first put into practice. The money used in carrying out modern methods in the many fish hatcheries is efficiently expended so far as the writer has been able to determine. The fundamental scientific problems involved have been solved so that the regular fish foreman can successfully direct and supervise all of the steps in the process.

After the eggs have been hatched and the young fed for a certain length of time, they are distributed to the ponds and streams. The last act in the series is the one concerning which we know the least. In order to gain an insight into the actual conditions, a typical Adirondack pond was selected for study.

The whitefish is the only species that has become at all abundant as a result of the policy of the state. The fault does not seem to be connected with the number of fingerlings placed in this lake, for the state has, indeed, been

[1] Contributions from the Zoological Laboratory, Liberal Arts College, Syracuse University, C. W. Hargitt, director.

generous. The problem that confronted the writer was to discover the cause or causes for the obvious failure of this lake to support an abundance of fish after these thirty years of restocking.

In the study of the life of any given body of water or area of land, a number of fundamental relationships have

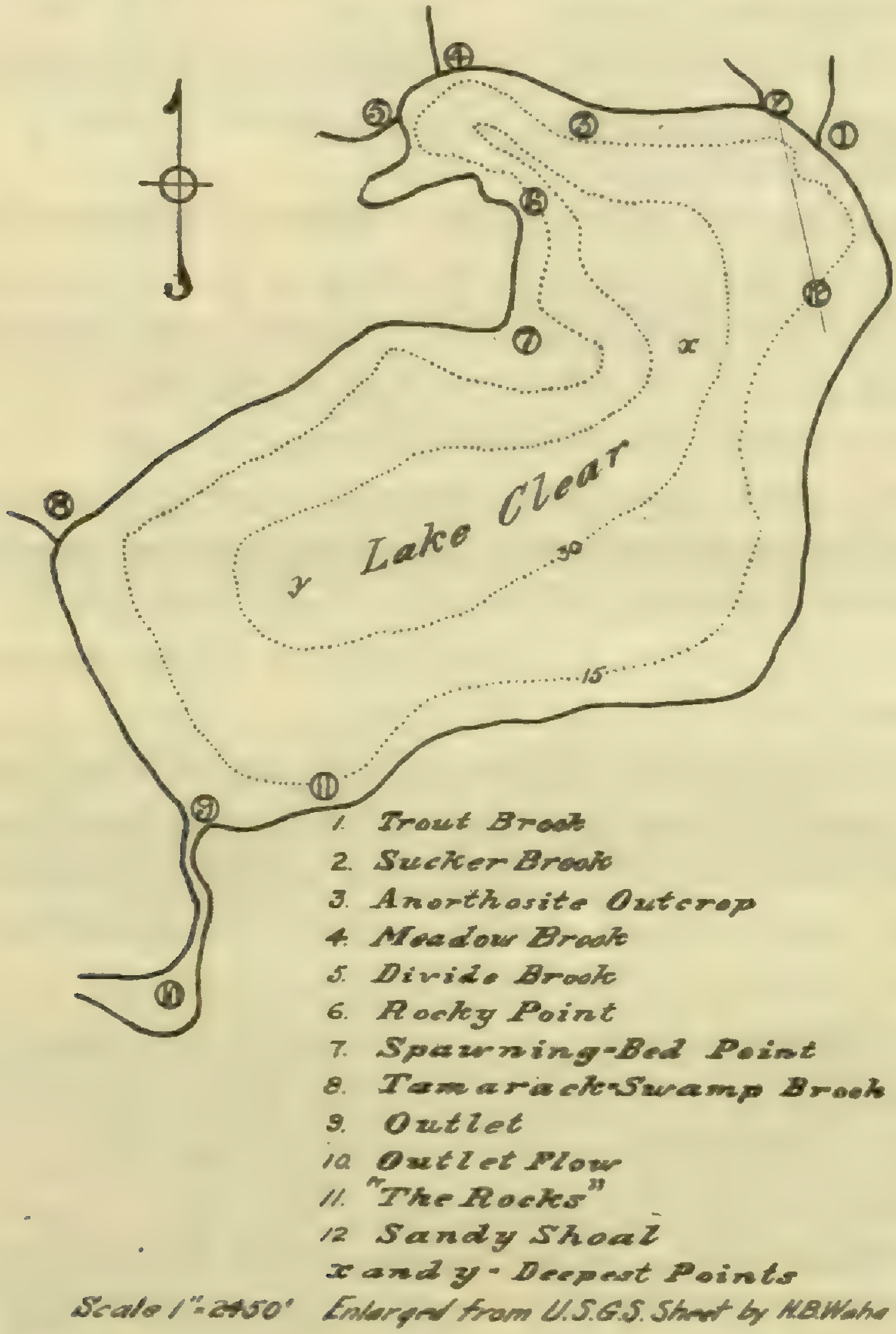

FIG. 1.

to be established before an effective detailed study can be made. After examining the conditions in several Adirondack ponds and lakes, the writer felt the necessity of examining the broader aspects of the problem with the hope that such a study might reveal some of the

causes that are influencing the present general food supply for fishes, the future food supply, the plant growth and other general problems related to the successful restocking of waters in the Adirondacks.

Such a study implies that one understand the soil and its origin. The Adirondack ponds are noteworthy for their abundance of sand. This sand is in the final analysis responsible for much of the modern life of these same ponds and lakes to-day. The geological history of the Adirondacks, especially its glaciology, is just becoming well understood by the experts. For the purposes of this paper it is simply necessary to keep in mind the fact that as the glacier receded, the Adirondacks were surrounded by a ring of ice. Within this ring of ice first the higher peaks and later the lower areas were exposed. The general result was that there were formed in succession a series of temporary glacial lakes, the remnants of which constitute the present Adirondack lakes and ponds.

Lake Clear, formerly known as Big Clear Pond, is located near Lake Clear R. R. Junction. It is at the headwater of the Saranac Lake system, so is free from the usual migration that takes place when one pond receives an outlet from another. The lake contains nearly 1,000 acres of water, which comes entirely from springs and mountain brooks. The water is clear, cool and pure—an ideal freshwater pond for restocking, one would say. What has thirty years of restocking by the state accomplished? The following table indicates that this pond has received 17,535,850 food and game fish.

In some regions, no less than eight successive lakes have been revealed by the recent critical studies of glaciologists. The net result is the accumulation of vast quantities of sand from which most of the organic food has been removed.

Lake Clear is one of the remnants of a much larger glacial lake, the shores of which are easily made out. This lake it has been proposed to call Lake St. Germain.[2]

[2] From the unpublished account of Lake Clear by Mr. Harold Alling.

FISH PLANTED IN LAKE CLEAR

	Brook Trout	Lake Trout	Rainbow Trout	Brown Trout	White Fish
1887	20,000	30,000			
1888	20,000	50,000			
1889	40,000	150,000		5,000	
1890	25,000	100,000		1,000	
1891	25,000				
1892	20,000	100,000			
1893	20,000	100,000			
1894	15,000	15,000			
1895	35,000	50,000			
1896	35,000	50,000			
1897	11,000	10,000			100,000
1898	1,600	10,000			
1899	5,000	10,000			
1900	36,000	35,000	3,000		600,000
1901	25,000				250,000
1902	750	25,000	5,000		800,000
1903	9,500	10,000	3,000		1,000,000
1904	18,000		8,000		1,000,000
1905	15,000	18,000			1,000,000
1906		50,000			1,000,000
1907	5,000	50,000			760,000
1908	138,000				800,000
1909	14,000	14,000			1,000,000
1910		20,000			178,000
1911		35,000			1,000,000
1912	10,000				1,500,000
1913	25,000	15,000			700,000
1914	55,000	25,000			1,000,000
1915	30,000	30,000			1,500,000
1916	30,000	65,000			1,500,000
	683,850	1,067,000	91,000	6,000	15,688,000

UPPER SARANAC, N. Y., (Signed) MILO F. OTIS
September 30, 1916

Its total area was possibly twenty times the present size of Lake Clear and included the present St. Regis lakes as well as several others. Preceding this fossil lake there was a still much larger lake more than twenty-five miles long. The station at Lake Clear and all of the level area extending north to Gabriel's Station is a small part of the floor of this large lake.

These conditions as outlined for Lake Clear in a general way apply to nearly all of the Adirondack lakes and ponds. Using Lake Clear as a center, there are in a circle, the radius of which is fifteen miles, more than seventy-five similar ponds and lakes, many of which are restocked by the state, so that the following study may

be taken as describing typical conditions in the large area of the Adirondacks.

Inasmuch as the past as expressed in the present physiography has played such a large part in influencing the present life of the lake, a brief description of the present conditions is necessary as well as the special stations at which collections were made. The names of these stations are found in Fig. 1. To these should be added the names of the two small bays, one centering at station 5, which we will name Big St. Germain Bay, and the one south of this, which we call Little St. Germain Bay.

FIG. 2a. The shore between stations I and II. The beach is modified every spring by the ice. Note how free from vegetation this strip of the beach is clear up to the boathouse.

The plant life, the ultimate source of fish food, is limited to the area between the shore and the 15-foot contour line except for the floating algal forms. This is the part of the lake, then, that is important for our study.

From just west of station 2 to half-way between stations 4 and 5, the shoal is composed of rocks and sand. The rocks are from the glacial till and similar to the soil conditions in the "fossil" shore of Lake St. Germain as exposed by the road east of the hotel. In front of Lake Clear Inn at station 3, the glacial till and sand have been washed away, leaving a small exposure of anorthosite rock. Around stations 6 and 11 large rocks and glacial till are common. The character of the soil in these three areas determines the spawning habits of at least three

FIG. 2b. The shore opposite station XII.

species of fish in the lake. The remaining part of the shoal around the lake is wholly sand derived from the anorthosite rock. Station 7 is a sand point, designated as Spawning-bed Point on the oldest maps, although the frost fish are the only ones that are known to spawn there now.

The high water of early spring and the strong southwest winds cause the sand to be removed from under the trees and shrubs on the north and east shores. As the ice breaks up in May, a strong southwest wind frequently forces a large amount of ice on to the northeast shore and on the north side on to the road. On the east half of the

north shore these ice-push shores form nearly every spring, to be later washed into the lake by the heavy rains of summer. These constantly shifting shores prevent permanent vegetation, thus tending to give a barren appearance to much of the shore lines, Fig. 2*a*.

The easily modified shore extending for the most part around the six miles of shore line may be taken as a good indication of the lake bottom adjacent to it. The wave action is constantly forming sand ripples which are as constantly being changed by a heavy rain or a different

Fig. 3. Station 1, Mouth of Trout Brook. During most of the summer except after a heavy shower, the water in this stream at this place is not over six inches deep.

direction of the wind. This makes it difficult for plants to gain a foothold even if the sand were good soil for them to grow in. The general result is, then, that most of the shallow water is free from any but a very limited plant growth.

The largest brook, station 1, Fig. 3, receives several tributaries from Big Clear mountain and flows into the lake the year round. The remaining brooks, especially Sucker, Meadow and Tamarack, frequently become en-

tirely dry during August. But after a severe rainstorm all of the brooks carry a large amount of water, often more than double their normal flow, for from twelve to eighteen hours, when they return to the normal again. Thus again the large amount of sand in the soil in this region plays an important part in determining how long the water shall be retained before it runs off. After these rains the water in the lake around the mouth of the brooks is colored dark by the organic matter brought down by the water of these streams. Two important results follow: First, as this organic matter settles to the bottom, a richer soil for plant growth is furnished; and, secondly, fish tend to come to these places for their food. The amount of water flowing from Trout Brook and the frequent strong winds constantly shifting the sands prevent plants from becoming established at this place. But the water is so dark here and so much cooler that this is by all means the best place to angle for brook trout, especially by fly-casting.

The summer food of fishes has been studied by so many investigators that the main facts for the several species are fairly well understood. But the more difficult problem of determining what the available food is during the winter and what fish eat during this period is still practically unknown. One naturally thinks that all aquatic life, like the deciduous trees, perhaps, enters into a resting state for several months, but that this assumption is far from correct can be shown by the following observations.

Through the courtesy of Milo Otis, superintendent of the Saranac Inn Hatchery, I have had sent to the zoology department a large number of the so-called red hydra, each month beginning with November and ending with April. These red hydra come into the hatchery tanks through the intake pipes in Little Lake Clear. These pipes are from 30 to 40 feet below the surface of the water. The important fact is clearly established that this very simple organism, sensitive to temperature changes, lives

throughout the year and actively forms buds in January, February and March in the Adirondack waters. Microscopic sections of these hydra taken in February reveal the presence of minute Entomostracans in the enteron. Some of these minute Crustaceans taken from a jar containing the hydra were submitted to Dr. C. D. Marsh for identification. He reported that they were *Cyclops americana*. As cyclops is the common food of hydra we may assume that this species, which is very abundant, is eaten by these red hydra. At any rate, hydra feed on minute animals so that animal food is a prerequisite for their active growth.

The food of the cyclops in turn is the minute floating algal plants. These must be in relative abundance in order to support so many of the minute Entomostracans. Thus the conclusive proof of the active, reproductive habit of these red hydra throughout the winter establishes the winter active life of cyclops and unicellular algæ in Little Lake Clear.

These observations indicate a greater amount of vital activity in such cold regions as the Adirondacks than we had been led to believe existed. If these minute and simple forms of life live throughout the winter in an active state, we may safely predict that most of the other forms of life except the larger plants are also active and that the winter food of fishes is probably similar to that of the summer in many particulars.

During the summer of 1916, I had opportunity to observe the habits of the red hydra which are common in Lake Clear, particularly at station 12. A number of collections were made early in the summer and I attempted to bring some of the live animals back to the university, but in each instance the hydra died before reaching the city. I then tried to acclimate them to aquarium life, placing them in regular aquaria jars in the boathouse, but in each case the hydra died in from twenty-four to forty-eight hours after being taken from the lake. As they were kept in the lake water, the only explanation that

seems applicable is that the water became too warm for them. During these same days, hydra were coming into the hatchery troughs at Saranac Inn and reproducing in such abundance that it was necessary to clean out the troughs every three days.

In these hatchery troughs, they grow so thick that a perfect mat is formed, covering the bottom and sides in patches two or three feet long. In the center of these patches, the hydras become brown, and, if left for about a week, may become nearly white. They look as if they were dead, but when touched, contract. Hydra taken in late September in Lake Clear were all brown, with a few that were nearly white. This wide range in color is apparently due to metabolic changes taking place in the chloroplastic corpuscles.

The red hydra are a source of food for fish, for the trout in the hatchery troughs eat them after they become a few weeks old. On first hatching, the small trout are killed by these hydra. After trout fry have eaten freely of red hydra, their droppings are colored red, indicating that the chloroplasts are not broken up in digestion. Doubtless the young fish in the lake and small minnows that secure their food from the stems of plants eat many of these hydra.

A further question arises in the relation of the fish to the several physiographic conditions in the lake. This is determined by classifying the fish habitats. These are stream, barren sandy-shoal, barren stony-shoal, vegetative and deep-water.

There is no vegetation growing in the brooks except inside the bridge of Trout Brook where *Potamogeton robbinsii* and some filamentous algæ are found. At the mouth of Meadow Brook a few bullrushes and pond lilies are seen; while the Divide Brook meanders over organic débris in which a few scattering plants of *P. robbinsii,* succeed in growing. There is a narrow fringe of yellow pond lilies about twenty feet from the mouth of this latter brook, and between the shore and this fringe of lilies a

few scattered plants of the seven-angled pipewort may be seen. Ordinarily the stream habitat furnishes the most favorable ground for vegetation, yet we see in these streams a dearth of species and a limited growth that clearly indicates limited and restricted food for such animals as live upon aquatic plants.

The barren sandy-shoal, the barren stony-shoal and the deep-water habitats are each almost entirely free from plant life. This leaves the vegetative to supply the necessary food. Aside from two patches of bullrushes and two small groups of yellow lilies, the vegetative habitat is restricted to the plants that form on the slope leading to the fifteen-foot contour. At station 12, for possibly an eighth of a mile, there is a thick fringe of aquatic plants composed of *Potamogeton prealongus* and *robbinsii*. In the southeastern part of the lake and also near station 8 two other thick areas of plants occur. These consist of Potamogetons, with the addition of a third species, *P. oakesianus*. Of the possible four miles of this slope around the lake not more than one sixth supports plants.

The study of these habitats then shows that the fish are limited to the vegetative habitat in their search for such food as lives in turn upon aquatic plants.

In order to determine what the fish were actually living upon, a study of the stomach contents was made, of which the following is a summary:

Salvelinus fontinalis Mitchill. Brook Trout.—The black-striped minnow (*Leuciscus carletoni*), grasshoppers, crayfish, snail (*Campeloma decisa*), a few insect larvæ and a pumpkin seed made up the diet of the twenty stomachs examined.

Eupomotis gibbosus Linnæus. Pumpkin seed. Collected at station 8, 20 to 25 mm. long.—Daphnia and cyclops with an occasional insect larva. Fish of the same size from station 5 were feeding entirely upon daphnia and cyclops. Judging from the number found in some of these fish, I would estimate that these small fish must eat more than 1,000 crustacea daily. One specimen had

more than 100 rotifers which belonged to the species of *Hydatina*. In all, about one hundred of these small fish were studied from various stations in the lake and all were found to be eating the same food, with but a small amount of individual variation. The same is equally true of the adults of this species.

Ameiurus nebulosus Le Sueur. Common Bullhead.—The bullheads in Lake Clear vary their diet, as plant remains, crayfish, clams, snails, plumatella and daphnia are all found.

Catastomus commersonii Lacépède. Common Sucker.—Plant remains, crustacean skeletons, sand, plumatella and débris are all found.

Notropis cornutus Mitchill. Shiner.—Daphnia and insects constitute their diet. A number were found with honey bees in the stomach.

Leuciscus carletoni Kendall. Black-striped Minnow.—Insect larvæ, rotifers, algæ, plumatella and daphnia were all found.

In view of the importance of the whitefish as food fish the details of this study are given.

Coregonus clupeiformia Mitchell. Common Whitefish; Labrador Whitefish.—These whitefish are by all means the most numerous fish in the lake, as from three to four thousand are taken in the fall nets at once. More whitefish are caught than all of the other species combined, so far as my observations go. One would naturally expect, then, that more of dead whitefish would be found along the shore than of any other species. If one happened to make his observations just when the whitefish are dying, the above would be correct; but not more than two or three times during a summer are any considerable number of whitefish to be found dead upon the shores. The following notes illustrate this point.

Dead whitefish collected between September 19 and 24, 1916, just as they drifted onto the north shore between the small brooks stations 1 and 2, and the East Flats, give the daily record as follows: September 19, two males,

$12\frac{1}{2}$ and $8\frac{3}{4}$ inches long; September 22, 4 whitefish from shore; September 23, 5 whitefish from shore; 3 others partly eaten by crows. All of these eight fish appear to be in a healthy condition and show no evidence of starvation; September 24, 5 more whitefish from shore. The intestines of three others were taken as the body of the whitefish was already mutilated by crows. During this week a strong southwest wind blew.

On July 2 and 3 a similar series of dead whitefish was found on this same stretch of shore. A dozen fish were noted, all of which were between 12 and 15 inches in length. These had all been partly eaten by crows when first observed, so that it was impossible to learn anything about their food. The crows begin their attack upon the body in the gill region and drag out the viscera through this opening. After the visceral delicacy is eaten, the dorsal muscles are gradually removed. The crows take from two to three days to eat up a whitefish. None of these twelve fish was poor or showed any sign of starvation. A strong southwest wind had been blowing for several days.

During the past ten summers I have noticed a similar series of conditions. Two or three times each summer, a large number of whitefish are found dead on the northeast shore. Occasionally, I have noticed the skeletal remains of whitefish on the west and south shores. During these irregular times when whitefish are drifting on shore, there are more of them than suckers, bullheads, brook or lake trout. Rheighard ('13, p. 224) says:

> Great numbers of dead suckers are thrown up on the beach in South Fishtail Bay in July and August. Many of these have the characteristic form of starved fish. The back is thin and sharp instead of round, and the head is disproportionately large compared to the body. . . . The emaciated fish do not appear to be diseased and are not usually parasitized heavily enough to account for their emaciation.

Colbert ('15, p. 35) names five causes of death in fishes, as follows: (1) Mechanical injury; (2) injury through attacks of other species; (3) the beaching of individuals

while pursuing or swallowing prey; (4) the accidental beaching while attempting to escape enemies; (5) disease and parasites.

These are the two most important of the recent observations on death in fishes. The size and general healthy condition of the whitefish collected eliminate all but the first cause given by Colbert. It is well known that whitefish are easily killed by handling and do not have the tenacity of life so characteristic of suckers or bullheads, for example. The whitefish, although occupying the deep basins of the lake, frequently come to the surface to play. On a calm summer evening one can hear them as they spring out of the water. The splashes which they make are more numerous in the deep water, while the brook trout are seen in shallow water near the mouth of the brooks. This is a common habit of whitefish in Lake Clear, especially during July and August. That they come to the surface is also shown by the fact that at times many are caught with not more than six or eight feet of line. Their habit of coming to the surface makes it possible to see how wave actions might cause their death. None of the other causes cited by the observer quoted explains the death of these whitefish. In the detailed study it was found that all of the dead whitefish collected this summer were males, which renders it all the more difficult to understand how wave action may be the only cause of death.

The following study of the stomach contents of these dead whitefish throws a good deal of light upon their food habits:

No. 1. Male. Length 11¼ inches. Intestine full of food. Stomach contents badly macerated and most of it impossible to identify. Apparently almost entirely *Daphnia kahlbergensis*. No copepods. The mesentery contained a large amount of fat.

No. 2. Male. Length 11½ inches. Stomach and intestine contain many minute crustacean skeletons. The remains of three honey bees covered with saprolegnia. A small amount of fat in mesentery.

No. 3. Male. Length 12½ inches. Stomach and intestine contain numerous minute macerated crustacea. Mesentery loaded with fat.

No. 4. Male. Length 11¾ inches. Thousands of minute macerated crustacea in stomach and anterior part of intestine. Remains of three honey bees. Small amount of fat in mesentery.

No. 5. Male. Length 12 inches. One honey bee. No fat in mesentery.

No. 6. Male. Length 11 inches. Numerous *Daphnia kahlbergensis*. No copepods.

No. 7. Male. Length 12 inches. One honey bee. Large amount of fat in mesentery and around stomach.

No. 8. Male. Length 11½ inches. Stomach empty. Intestine partly full of digested food. Large amount of fat.

No. 9. Male. Length 11 inches. Stomach contained numerous *Daphnia kahlbergensis* and *Leptodora hyalina*. No copepods. The intestine was 5 inches long and $\frac{5}{16}$ of an inch in diameter and was packed full of cladocera skeletons.

The food in numbers 1, 6, 9 were identified by Dr. C. D. Marsh. It is probable that the minute crustaceans noted in 2, 3, 4, 8 are the same as those found in 1, 6, 9. This material was so badly macerated that it was impossible to be confident of the identification.

The large amount of food found in the stomach and intestine, and the presence of a great deal of fat in most instances, is convincing evidence that these fish did not starve to death. It seems strange that they were all males. The honey bees eaten had evidently been in the water several days, as practically every one was covered with saprolegnia.

The following whitefish were collected by Milo Otis, superintendent of the Saranac Inn Hatchery. The fish were taken during November, 1916, in nets used to secure spawning fish.

No. 10. Male. Length 11 inches. Stomach empty. Duodenum contained minute crustacea, too macerated to identify. In the intestine were found numerous winter eggs of *Daphnia*. These winter eggs appear to be uninjured by the digestive enzymes. Some were found in the rectum in a perfect condition, so that I feel confident that most of them pass through the digestive canal and into the water ready to grow into *Daphnia*. This is an important fact when the problem of an adequate amount of food is taken into consideration.

No. 11. Female. Length 11½ inches. Stomach empty. Macerated cladocera in intestine. Many tapeworms present.

No. 12. Male. Length 11½ inches. Stomach empty. Intestine contains macerated cladocera. Very fat.

No. 13. Female. Length 11 inches. Stomach and intestine mostly empty. Parasites present. Ovaries full of eggs.

No. 14. Male. Length 11 inches. Stomach empty. Intestine with cladocera skeletons. Parasites present.

No. 15. Female. Length 8½ inches. Stomach and intestine empty. Cœlome full of eggs.

The following viscera taken from whitefish collected by Milo Otis were received November 24, 1916:

No. 16. Stomach empty. Several parasitic flatworms present.

No. 17. Stomach contained 3 pumpkin seeds (*Eupomotis gibbosus*) 1 inch long; 1 partly digested *gibbosus;* 1 snail (*Amnicola Limosa* Say identified by F. G. Baker). Parasitic flatworms present.

No. 18. Stomach contained many *Daphnia kahlbergensis* and *Leptodora hyalina.* No copepods.

No. 19. Stomach contained numerous *Daphnia* winter eggs; 8 whitefish eggs.

No. 20. Stomach full. One pumpkin seed (*Eupomotis egibbosus*) and 103 whitefish eggs. Parasitic flatworms present.

No. 21. Stomach empty, with many parasites.

No. 24. Stomach full of whitefish eggs.

No. 25. Stomach contained 1 partly digested fish, probably *gibbosus.*

Nos. 26, 27. Each contained many *Daphnia.*

No. 28. Stomach contained *Daphnia* and whitefish eggs.

In the jar containing the viscera of the whitefish numbers 16 to 28, there were, in addition to the above records, 20 pumpkin seeds that had been in some of these stomachs and 107 whitefish eggs. 33 tapeworms were also found in this residue.

Small pumpkinseeds were selected in order that the food habits of very young fish might be compared with the adults. Small fish 20 to 25 millimeters (about an inch), 25 to 30 millimeters, and adults 100 millimeters long (3 to 4 inches) were examined.

These young fish live almost exclusively on small cladocerans, with cyclops and daphnia predominating. Occasionally one was found having only rotifers. Insect larvæ do not play an important part in their food so far as my studies go. The adults include, in addition, plants and *Plumatella.*

Baker (1916, pp. 184–188) gives a summary of the facts of the food habits of this species in which insect larvæ and mollusca are seen to be the most important. In Walnut Lake, Wisconsin, insect larvæ are mainly eaten;

while in Douglas Lake, Michigan, and Oneida Lake, New York, molluscs are the more important. In Lake Clear, cyclops and daphnia may be said to be their main food. These two animals happen to be almost the only food of the whitefish. The pumpkin seeds in Lake Clear thus become a hindrance in the stocking of this lake. The number of pumpkin seeds eaten by other fish does not appear to be large. It is suggested that food fish which live harmoniously with whitefish but feed upon pumpkin seeds would make a valuable combination.

Forbes (pp. 108, 1883) made numerous experiments to determine the natural food of young whitefish. He found that cyclops were more important than all the other organisms combined. Hankinson (p. 239, 1914) also noted the almost exclusive diet of cyclops and daphnia. Baker (pp. 159–161) shows that not only crustacea, but molluscs are important as food for adult whitefish. My observations emphasize the limited diet of large whitefish in Lake Clear where cyclops and daphnia are all that are eaten during the summer. In the fall some specimens were taken with the snail *Amnicola* in the stomach, but this snail is present in limited numbers only, so can not be very important as a source of food in Lake Clear. During the fall, small pumpkin seeds and their own eggs are added to the daphnia-cyclops diet. It is to be noted that all of the dead whitefish were in good condition, most of them being fat. These all fed upon the daphnia-cyclops diet.

These cladocerans produce winter eggs in large numbers which are not destroyed by the digestive juices of the whitefish nor the other fish that feed upon them. These eggs pass through the entire digestive canal uninjured. This is an important factor in keeping up the number of these minute organisms. Were these winter eggs digested and used as food, it is probable that this, the most important source of food for whitefish, would soon become exhausted.

The brook trout taken in Trout Brook or at its mouth

feed for the most part on insects; while those taken in the lake eat minnows almost exclusively. The two taken early in the spring (the ice did not break up until after May first) had been feeding upon pumpkin seeds, crayfish and insect larvæ. No molluscs were found.

The food of the three species of minnows examined as well as the suckers indicates that these fish live largely on the same animals as the whitefish and the pumpkinseeds. The bullhead is the most general in its diet of any of the fish studied, taking clams, snails, crayfish, minnows and plants.

A detailed study of the food habits of the fish in any lake is necessary before one can tell just what the several species of fish actually eat. It is to be regretted that in this lake the number of organisms suitable for food for fishes is so limited. The result is that each species comes into competition with the other species for food. *The result of this competition for the one abundant food, daphnia-cyclops, prevents this lake from permanently having large numbers of food fish.*

The consideration of the history of the lake, the specific habitation of the fish, the noteworthy dearth of aquatic plants, the actual food of the fish and the restocking that has taken place during the past thirty years leads to the conclusion that restocking has not been and cannot be a success. In estimating how many fish any given body of water will support, one must first consider the variety and abundance of aquatic plants. *There can not be any more animal food for the small fish and fingerlings than can find subsistence on the aquatic plants of any given body of water.*

In this connection a second question might be asked, why stock any Adirondack pond with a distinctively food fish? Whitefish when not taken in nets are caught at baited buoys which are placed early in the spring by the local fishermen. I have counted 25 buoys scattered around the lake in early June. At these buoys a considerable number of whitefish are taken by relatively very

few people, probably not over fifteen separate families. Sportsmen who desire to fish for whitefish employ some one who has a buoy located advantageously as a guide. This guide ties the boat to his buoy. In a half day, from six to twenty whitefish may be thus taken. No one is expected to tie to one of these buoys without the "owner's" consent. The result then of this extensive stocking by the state has been to enable a few local families and guides to catch for their own use and to sell a few whitefish. The general vacation transients are not benefited nor is this excellent food fish taken in such numbers as to yield any considerable amount of food. If the state is to continue to restock such ponds as Lake Clear with whitefish, then some better method should be devised to take the whitefish.

The fundamental reason why the extensive restocking of Lake Clear has not been a success is due to the glacial origin of the lake. The mere fact that the sand in which the plants try to grow has been resorted by the glacial waters until most of the organic material, plant food, has been washed away, produces a very limited number of aquatic plants. Such plants are indispensable as a source of food for the numerous minute organisms upon which fish normally feed. One can hardly appreciate what a large number of different animals fish eat unless he has given careful study to this problem. Baker (pp. 157–199) gives a summary of the different kinds of animals eaten by fish and the variety is in striking contrast to the one abundant group of organisms (daphnia-cyclops) in Lake Clear. In order to have a general growth of fish in a lake, I believe that an abundance of *several kinds* of fish food is indispensable. The conditions in Lake Clear well illustrate how the species that can most successfully utilize the form of food that is abundant survives and greatly increases in numbers, while the others remain few in numbers.

The shores of Lake Clear are remarkably free from dead fish and one rarely finds any dead fingerlings. It

would seem as if there were but one conclusion, namely, that the most of the fingerlings are eaten by larger fish.

The probabilities are that there would not, then, have been any more trout in Lake Clear, even if the state had placed many more than it has during the past thirty years. This lake really illustrates an instance of overstocking simply because there was not an adequate amount and variety of food. At present there does not seem to be any way to remedy this deficiency.

During the past summer the states have been urged to increase greatly their production of food and game fish. This very general recommendation fails to recognize certain fundamental facts. The next step in advance along fish propagation is one that will have to be taken slowly, as it necessitates a great deal of critical information. It is becoming more and more apparent that we must not only know the breeding habits of the small minnows, pumpkin seeds, etc., the fry of which serve as admirable food for the food-fish fingerlings, but also the natural history of all of the life of a given body of water. It is a well-recognized biological axiom that no organism can live unto itself alone. This applied to our problem means that a clear and adequate supply of water is not the only factor that must be considered in deciding to restock great bodies of water with fish-fry. But rather the intricate and more or less obscure conditions that determine the sum total of life in each body of water must be taken into consideration. Such studies alone furnish a correct basis for determining the extent to which an animal may draw upon a given source of food, upon the available body of food, and many kindred problems. Before the state can wisely undertake to place more fingerlings in the ponds, it ought to know whether there is enough available food to keep them at least from starving.

The extensive restocking of most of the Adirondack ponds is done mostly for the benefit of the sportsmen. The benefit that has accrued to these and many other vacationists is very great, but one can not help wondering

if this policy should not be restricted and adjusted. One or two trout hatcheries would probably be able to produce all of the trout needed, while the rest might be turned over to the production of food fish which should be placed in the larger bodies of water that support an abundant aquatic plant life. The conditions in Oneida Lake are in such striking contrast to those in the Adirondacks that one can unhesitatingly suggest that this lake could support an incredible number of fish.

Intimately associated with this general problem is the question of disease in fishes. Under this heading are included the several forms of parasitism. Reference will be made to two or three only. This is the field in which the greatest progress has been made in the cure and prevention of the diseases affecting man. But before *prevention can be applied, the life history of the parasite must be understood.* In the main, the work of the national and state governments has been confined solely to hatchery problems. Here is a field that they should enter, as many of the problems are too large and involve too much expense for the individual.

Salmincola edwardsii (Olsson).

This parasite belongs to the copepod group of crustaceans, many of which are familiarly known as "fish-lice." Wilson says: "This family (Lernæopodidæ) of parasites is widely distributed amongst fishes in both salt and fresh water. Some of our best food and game fish are infested with them, and when they once obtain entrance to a stock pond, fish hatchery, or aquarium they usually multiply so rapidly as to become a serious nuisance, and may even kill the fish" (p. 569). There are some one hundred and thirty-six different species of animals that belong to this family, all of which are parasitic during their adult life. In the genus to which our specimens belong, there are twenty species, eighteen of which live exclusively upon the several kinds of trout.

Salmincola edwardsii is found exclusively infesting the brook trout (*Salvelinus fontinalis*). All of the specimens

taken in Lake Clear were attached to either the dorsal or anal fin. The gills of these fish were examined but no fish-lice noticed upon them. This seems strange as Fasten (1911–12) reports them as especially abundant upon the gills. They were found on trout ranging from four inches in length to those fourteen inches long, which were caught in Trout Brook, in the lake near the mouth of this inlet, station 1, and in the bay near station 5. They were taken upon both large and small fish in each of these locations. My specimens were collected during July, August and September. The last specimens were on a nine-inch male caught in Big St. Germain Bay, September 28, 1916. The egg-sacs were full of embryos.

This common "fish-louse" is easily recognized. From the main part of the body two large egg-sacs are suspended. With an ordinary hand lens, the numerous small embryos can be noted, and the small beak which attaches the parasite to its host. Fasten has recently worked out the life history and the habits of this interesting parasite, which undergoes an extensive degeneration after becoming parasitic.

These parasites are widespread in the United States in the native trout streams, and in Canada and Europe. The first scientific record of this particular parasite is by Linnæus in 1761. It seems strange that an animal could be known for so long and its habits not be understood until within the past five years. The fact that it is so widespread and has been known for so long indicates that it is not a serious pest except under very favorable living conditions. These are best found in the hatcheries or stock ponds, where many fish live in a small enclosure. The numerous parasitic larvæ then have little trouble in finding a host. In the streams and ponds of this state, we need not fear that the trout will be killed by them. The chief reason is that the trout are few in numbers in any given place, so that when the embryo parasites make their escape, there is small chance of their ever becoming attached to a trout. The result is that each trout in a

wild state does not usually harbor more than a half dozen, and this number does no serious harm to the trout, especially where they are attached to the fins.

When this pest gets into a hatchery, but little can be done. The infested trout at the Wild Rose Hatchery in Wisconsin were treated with "solutions of copper sulphate, potassium chlorate, sodium chloride, and mixtures of sodium chloride and potassium chlorate, but these had no effect upon the parasite" (Fasten, 1911–12, p. 17). About the only remedy that is effective is to destroy all of the parasitized trout, which can be done after the spawning season; for there is no reason to believe that these parasites can be carried from one place to another except in the manner described by Fasten. We do not know how these parasites pass the winter, but in view of the fact that they are not known to eat during their free-swimming period, it is probable that those which live through the winter do so as parasites upon trout. During the cold weather the growth changes would not take place as rapidly, so that a given parasite might remain on a trout for five or even six months during the winter.

Clinostomum marginatum.

This is a small Trematode that lives for a part of its life embedded in the muscles of several food and game fish. The popular name of "grubby" is used to describe this condition. So little is known about this parasite that renders thousands of dollars worth of fish unsuitable for food that any new facts are welcome. In this connection, the following field observations are recorded upon this very annoying parasite. In an earlier paper (Smallwood, '14) attention was called to the fact that these worms may voluntarily leave the body of their host after the host dies. On May 28, 1914, about 50 perch were taken from McCauley Pond between Saranac Lake village and Lake Clear Junction. After returning to camp, it was noticed that these perch were "grubby" and they were all left in a pile on the ground. The next morning, I examined the pile of perch and was able to pick up more than 100 flat-

worms that had crawled out of their cyst during the night. If I had cared to do so I could have gathered several hundred specimens during the day as they continued to escape from the cysts.

This observation answers one question, namely, that these parasitic worms remain in the body of the perch all winter, as the worms were in the same stage of maturity as those taken in July, August and September. It further suggests, also, that *Clinostomum marginatum* may return to an aquatic habit directly from the body of the fish.

Guides and fishermen claim that perch are free from "grubs" at certain seasons of the year, a belief which I am unable to confirm. But if more extended studies show that their belief is true, the method by means of which the "grubs" leave the fish has been found.

So far as we know, these parasites are mainly confined to members of the bass and perch families, although a few cases are on record of trout being infested with them. Occasionally one finds a few bullheads that are "grubby." In Lake Clear *Lepomis gibbosus* and the minnows are largely infested by them.

I can also confirm my observations (p. 11, '14) that fish eating parasitized minnows are not themselves infected through this avenue. One brook trout was found with a partly digested minnow in its stomach. In the flesh of the minnow a dead parasitic clinostomum was observed.

I would say that the number of fish harboring this parasite in Lake Clear is on the increase.

The following observations upon some larval stages in Trematodes may help to start some one upon this problem without losing a season experimenting.

During the past three years, I have frequently found in the muscles of perch and pumpkin seeds minute cysts. Each of these cysts contains a larval Trematode.

The wall of the cyst is tough and easily "shells out" of the muscles, but is not readily penetrated by the ordi-

nary killing fluids. This has resulted in my not being able to secure suitable sections for detailed study. It will probably be necessary to make most of the observations upon living material, which will require that one have a microscope and microscopic reagents while doing field work.

The following general facts may help to direct attention to this important stage in the development of the life history of Trematodes. Possibly some fish containing them may be found near a laboratory and thus readily studied.

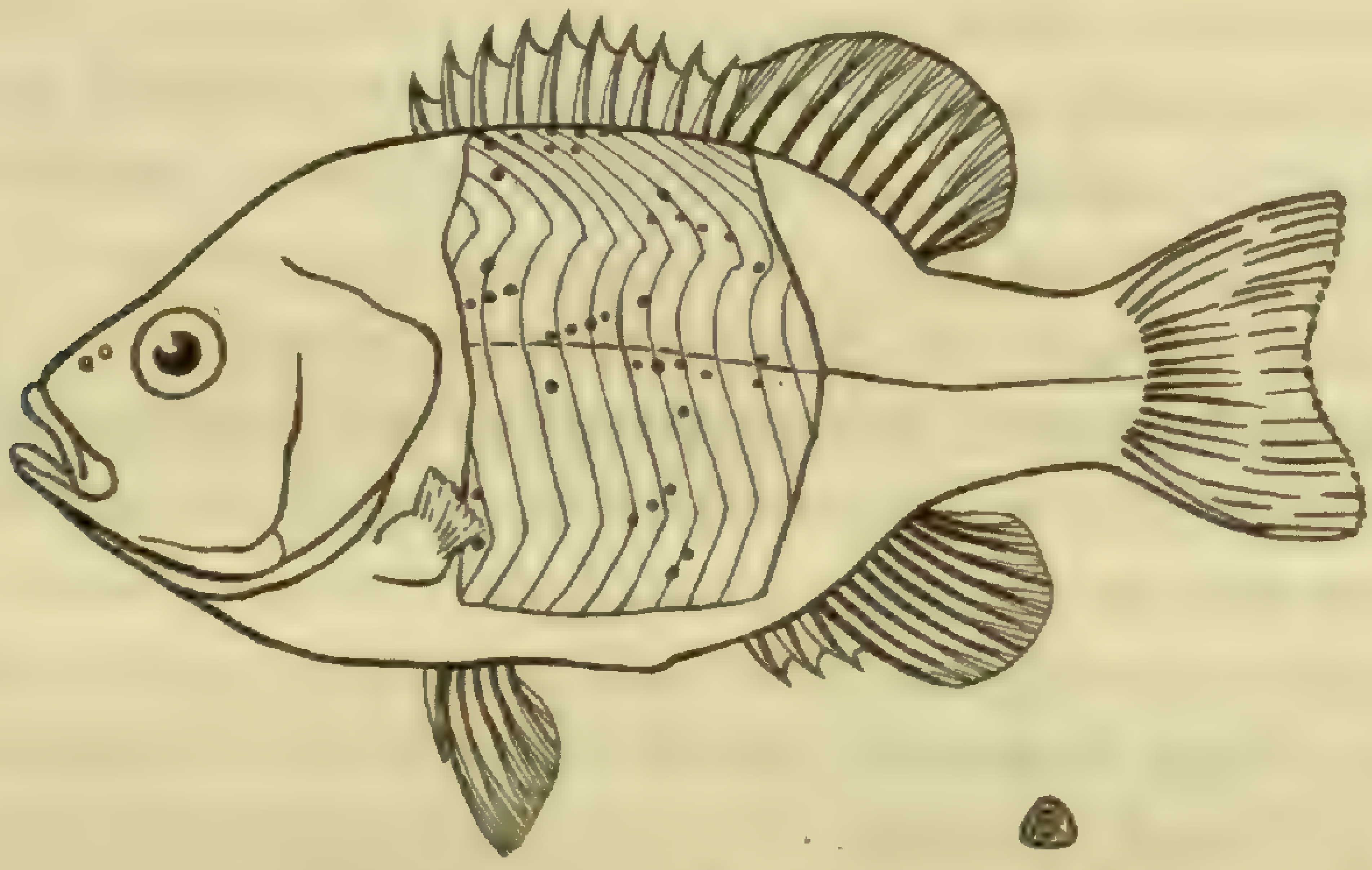

FIG. 4. *Lepomis megalotis* (Rafinesque), long-eared sunfish. Taken in Lake Clear, 1915. A portion of the skin has been removed to show the position that the larval stages of certain undetermined Distomes occupy in the flesh.

Fig. 4 shows the usual position of these larval stages in the muscles of the long-eared pumpkin seed taken in Lake Clear during July, 1915. Each cyst is accompanied by a small amount of pigment in the more advanced stages, although I have seen many of them with no pigment and nearly the same appearance as the muscle (Fig. 7). One must often pick the muscle fibers apart in order to find the cyst as most of them do not show on the surface. I have not been able to discover that they are found in any definite region of the body, although they are more numerous near the dorsal fin.

A photomicrograph of a young cyst shows a number of blood vessels entering one end of the cyst. The cyst

itself contains numerous blood corpuscles, as if they had been emptied into the cyst. The difficulties of fixation have prevented me thus far from studying the character of the blood in these cysts.

As the cyst grows, the wall of which is made up of connective tissue, partitions are formed which grow in from the main outside wall. The result is that in the older stages three to five separate cavities are found in each cyst (Fig. 6), although but a single larval Trematode is present in each cyst. I have opened a large number of these cysts and thus far have found no exceptions.

FIG. 5. The perch (*Perca flavescens*) showing minute distomes embedded in the skin and fins. These parasites can be recognized in the photograph as minute, black spots. The black pigment surrounds the parasite.

Not much can be said at this time in regard to the structure and changes through which this larva is passing. That it is growing there can be no doubt, as different stages showing the presence or absence of some of the mature organs were found. In most of the whole larvæ dissected and mounted, the excretory ducts are completely formed, while the digestive tract is limited chiefly to the anterior end. Two suckers can be recognized and a part of the reproductive organs. The whole animal is so very small that it can scarcely be seen with the unaided eye. It will require better fixation before the species can be determined accurately. I am inclined to

believe that it is the larval stage of either some species of *Holostomum* or *Clinostomum.* The latter is more numerous in this lake; but the size and pigment strongly suggest *Holostomum,* the adult appearance of which is shown in the photomicrograph (Fig. 7).

From the studies thus far made, I am inclined to think that it takes one season for this larva to transform into the adult worm. My reason for this conclusion is that

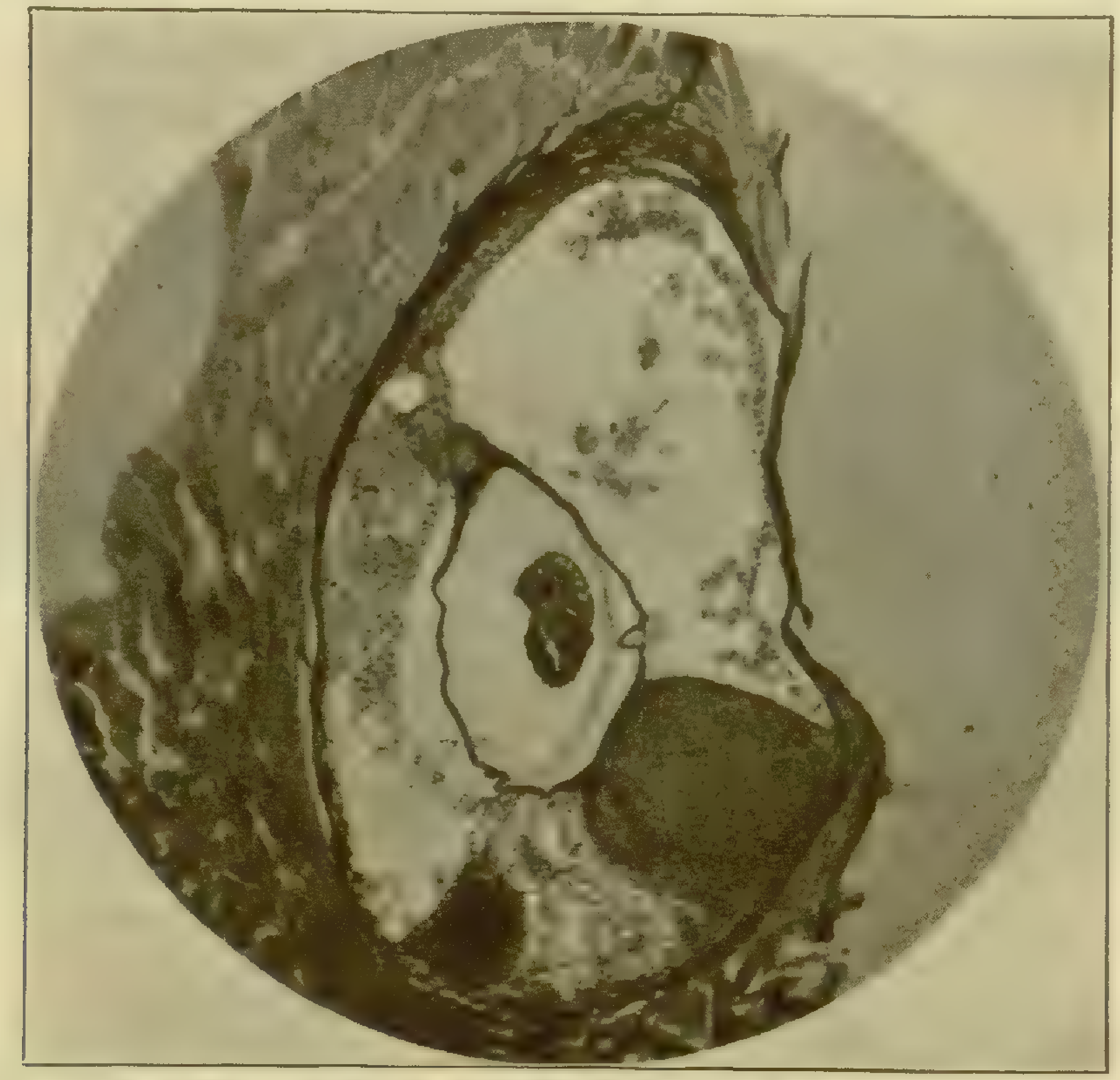

Fig. 6. Photomicrograph of the larval cyst of an undetermined distome. Each cyst contains but a single young worm, although there are several partitions. The cyst is surrounded by several layers of connective tissue and is embedded in the muscles.

there is so little difference between the several stages that I have secured.

In the hope of throwing some light upon the relation of Trematodes to fish, the writer urged several years ago that some "grubby" perch be placed in a separate tank in one of the hatcheries and fed for one year to see what happened, but the suggestion was rejected as not practical, although a number of specific experiments were out-

lined. It is unnecessary to say that many thousands of dollars' worth of fish would be rendered available throughout the United States, if this one disease alone could be prevented. Perch and bass which are so generally infected with Trematodes are delicious pan fish and usually easily caught in large numbers. It would seem as if the mere calling attention to this large amount of food annually wasted would stimulate some organization to finance the necessary scientific investigation. Such an investigation would need to continue at least two years and possibly longer; but the expense involved would be a small fraction of the returns, if the disease could be prevented.

"Grubby" perch are but one illustration of the diseases that occur in our fresh-water fish. There are a number of diseases due to bacteria and others caused by certain Soporozoa, Fig. 7. These diseases are usually epidemic,

FIG. 7. *Leuciscus carletoni* (Kendall), black-stripped minnow. Taken in Lake Clear, 1916. Infected with *Myxobolus*, a sporozoan parasite.

killing large numbers of fish in a few weeks. The main fact that is known now is that the fish die and several specific microorganisms are observed to be associated with certain ulcers, cysts, etc. But as to what causes lead up to the fatal termination of the diseases, little is known.

An admirable monograph upon carcinoma of the thyroid in the Salmonoid fishes was prepared, but left incompleted because of lack of funds. This is about the only serious study of fish diseases that has been made in the United States.

At this time, when all are anxious to help in whatever way that they can, it may be permissible to suggest that

scientists may render real service along the general lines indicated in this paper. To be more specific, they may be summarized as follows:

1. A critical study of the life of the fresh-water ponds and streams is very desirable.

(*a*) To determine the life history and food habits of the small fish and invertebrates present.

(*b*) To determine the amount and conditions of plant life—the ultimate source of food for all animals.

(*c*) To determine if more plants can be made to grow in water naturally lacking sufficient plant life.

(*d*) To determine if it is possible to introduce enough natural food for fry and fingerlings to keep them from starving, as many of them probably do now in such ponds as many of those in the Adirondacks.

(*e*) To determine to what extent the natural food of the fish is eaten by invertebrates living in the same waters.

When these problems are solved, the next step in efficiency in fish culture can be taken. It will require the cooperation of many scientists. The result will be the substitution of an intelligent method of restocking in place of the present one, which is often unintelligent or politically influenced.

2. A detailed study of the several diseases occurring in fish.

(*a*) It is necessary to know the complete life history of such parasites as the Trematodes before any one can formulate preventive measures. There are at present at least four different species of Trematodes found in our fresh-water fish and the complicated life history of each is unknown.

(*b*) The causes leading up to the usual epidemics in fish must be determined before these can be prevented. This is a problem for the bacteriologist and the protozoologist.

When these problems are worked out, an enormous amount of fish food will be conserved for human needs.

SYRACUSE UNIVERSITY,
October 29, 1917

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SHORTER ARTICLES AND DISCUSSION

MODIFICATIONS OF THE 9:3:3:1 RATIO

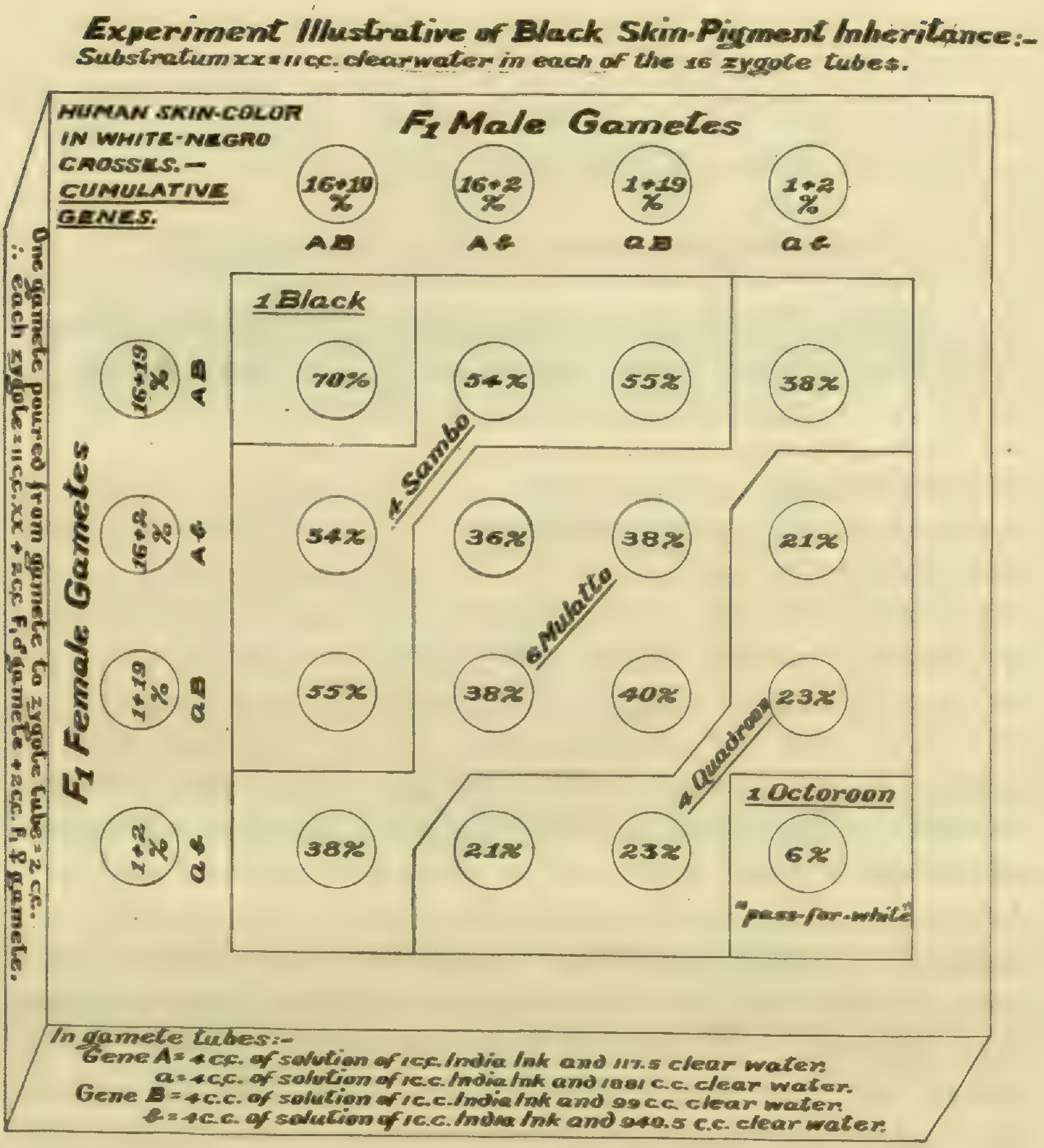
A. Chemical Experiments Paralleling the Several Possible Modifications of the Mendelian F_2 Di-hybrid Phenotypic Non-blending Ratio 9:3:3:1

The foundation F_2 di-hybrid ratio 9:3:3:1 consists of 9 individuals having somatic traits both "A" and "B," 3 individuals having "A" only, 3 having "B" only, and 1 having neither "A" nor "B." Or, if each allelomorphic pair consists, not in a gene and its absence, but in genic entities contrasted in quality or quantity and showing clean-cut dominance and recessiveness, in 9 "A" and "B" both dominant; 3 "A" dominant, "b" recessive; 3 "a" recessive, "B" dominant; 1 "a" and "b" both recessive. This di-hybrid ratio was one of the early discoveries of Mendel[1] himself, but after the revival of genetical studies in 1900 experimental breeding had not continued long before modifications of this ratio became apparent. Thus Bateson[2] mentions a number of cases in which the 9:3:4 F_2 ratio is found. It is apparent in such cases that two unit trait-pairs are involved, that the dominant phase of one of them standing without that of the other in 3 individual F_2 somas is not to all patent aspects different from the 1 individual possessing the dominant phase of neither of the two trait-pairs involved. In the gametes of individuals of families that produce the 9:3:4 ratio the segregation and recombination of genes are, however, just as clean-cut and follow the same rule as in pedigrees giving the unmodified foundation ratio 9:3:3:1; only the somatic working out of the genes is different in the two ratios.

Barring blending, linkage, crossing-over, non-disjunction, sex-limited inheritance and other special phenomena, which limitations preserve intact the numerical entities 9, 3, 3, and 1, the

[1] Mendel, G., "Experiments in Plant Hybridization" (reprinted in English in Bateson's "Mendel's Principles of Heredity," pp. 334–379), p. 351, 1866.

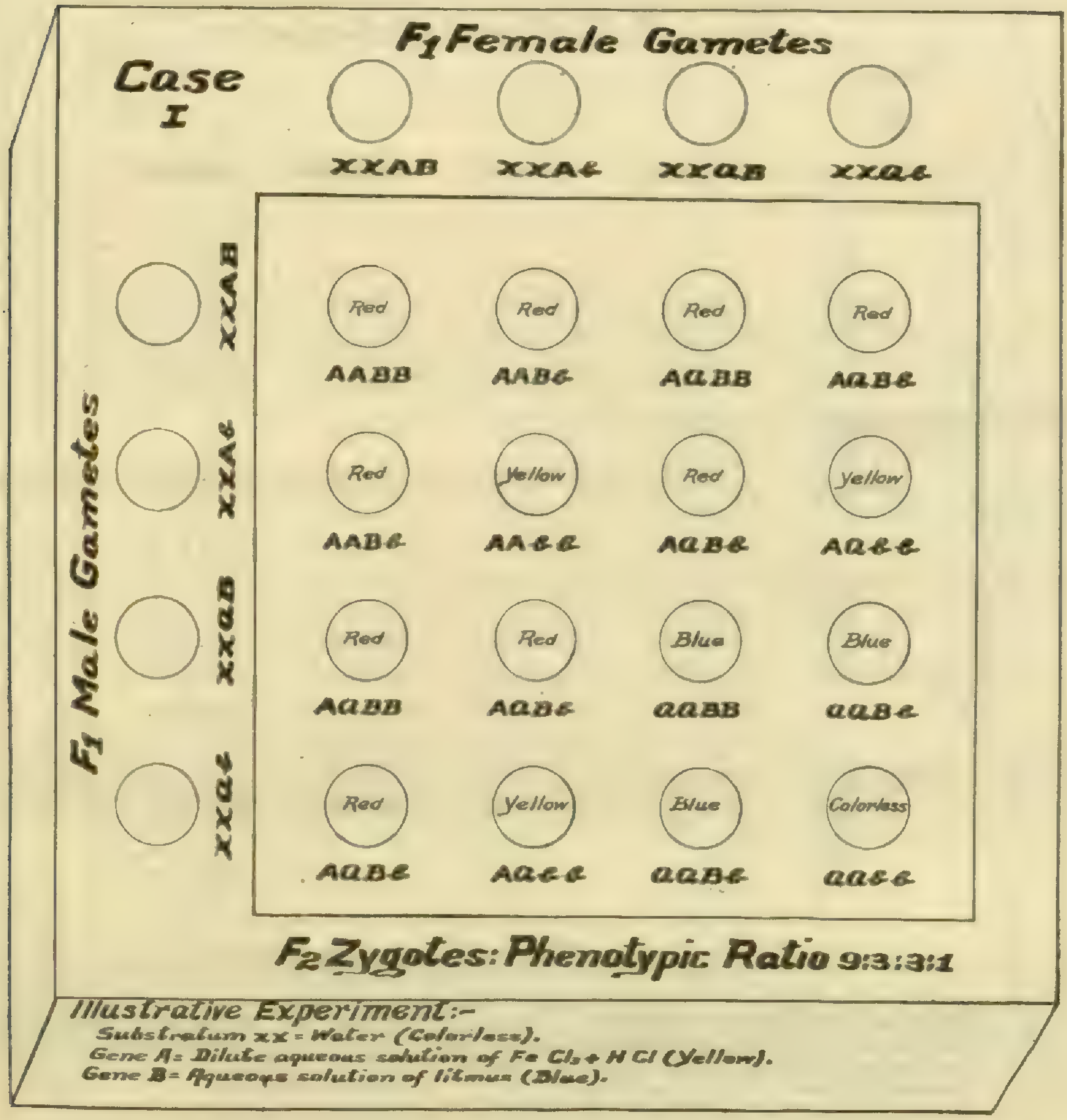
[2] Bateson, W., "Mendel's Principles of Heredity," p. 80, 1913.



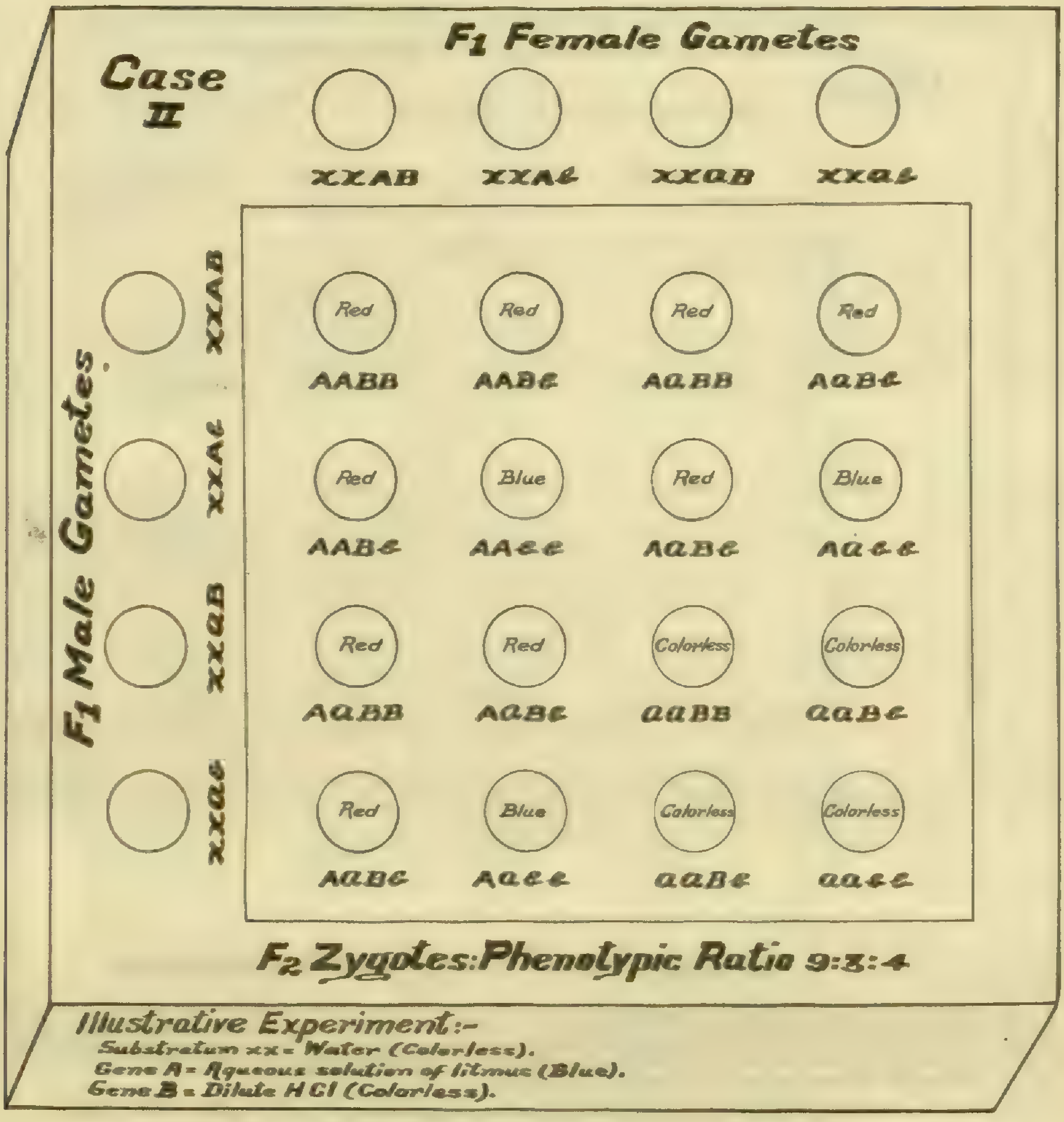
following table presents in orderly fashion all of their possible ratio-recombinations:

Series A

Case	I.	9:3:3:1.
Case	II.	9:3:4.
Case	III.	9:6:1.
Case	IV.	9:7.
Case	V.	10:3:3.
Case	VI.	10:6.
Case	VII.	12:3:1.
Case	VIII.	12:4.
Case	IX.	13:3.
Case	X.	15:1.

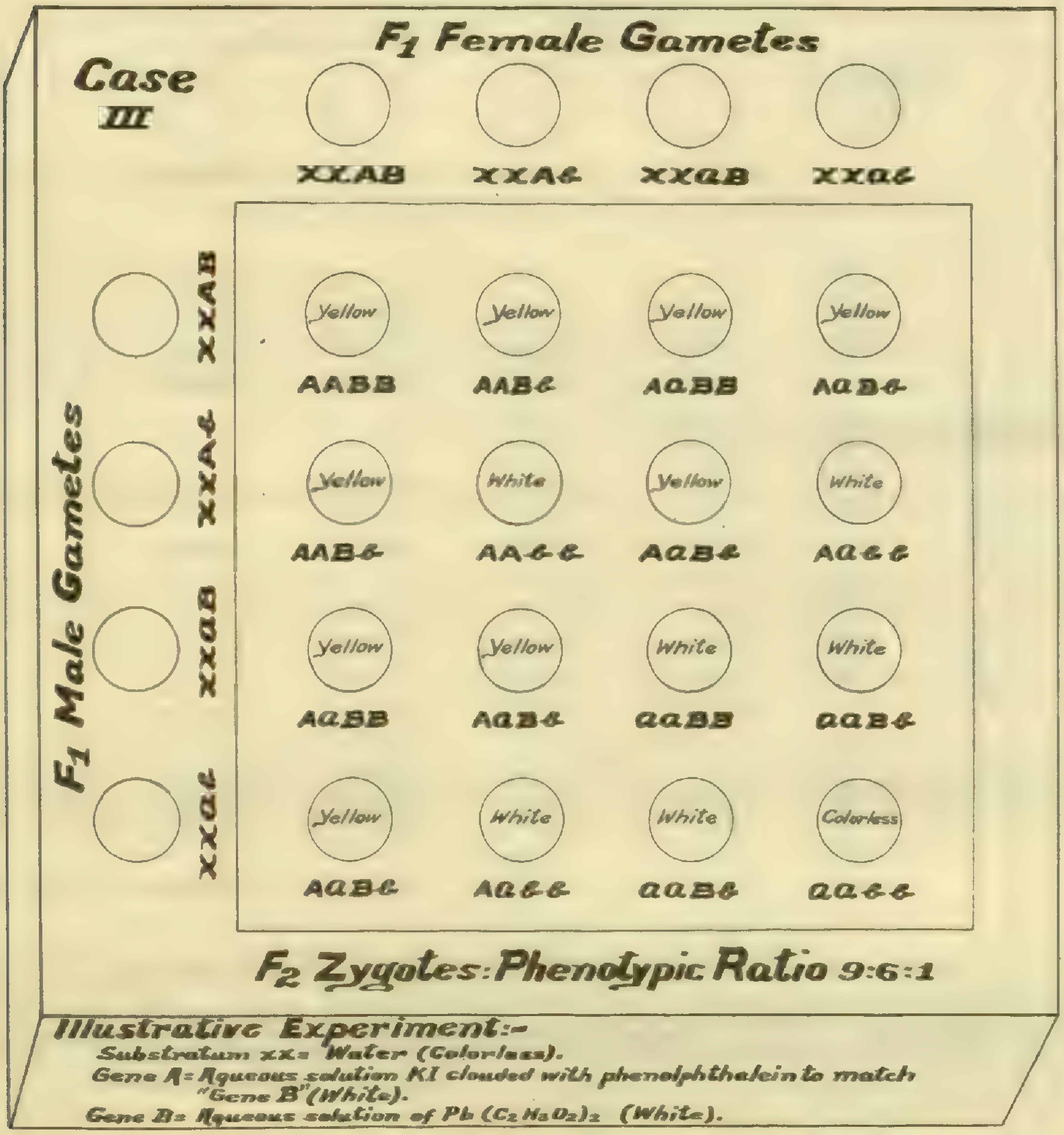


The chemical experiments described in the accompanying figures parallel chemically what must happen to the F_1 genes in their development into traits in the F_2 somas in each case of a modified somatic di-hybrid ratio. Each drawing represents a 2-inch wooden block $7\frac{1}{2}$ inches square, with twenty-four $\frac{5}{8}$-inch holes, $1\frac{1}{4}$ inches deep, suitable for holding test-tubes. The four holes at the top hold test-tubes containing chemicals representing the four types of F_1 female gametes possible when di-hybridism is being considered; the four to the left perform the same service for the four male gametes. The sixteen holes blocked off in the square hold test-tubes for the sixteen types of zygotes resulting, by the checker-board method, from all possible unions of the four male and the four female gametes. X X represent the substratum or the sum-total of hereditary qualities other than the traits under consideration. The lettering under each test-tube circle is the genetic formula for the gamete, or zygote as the



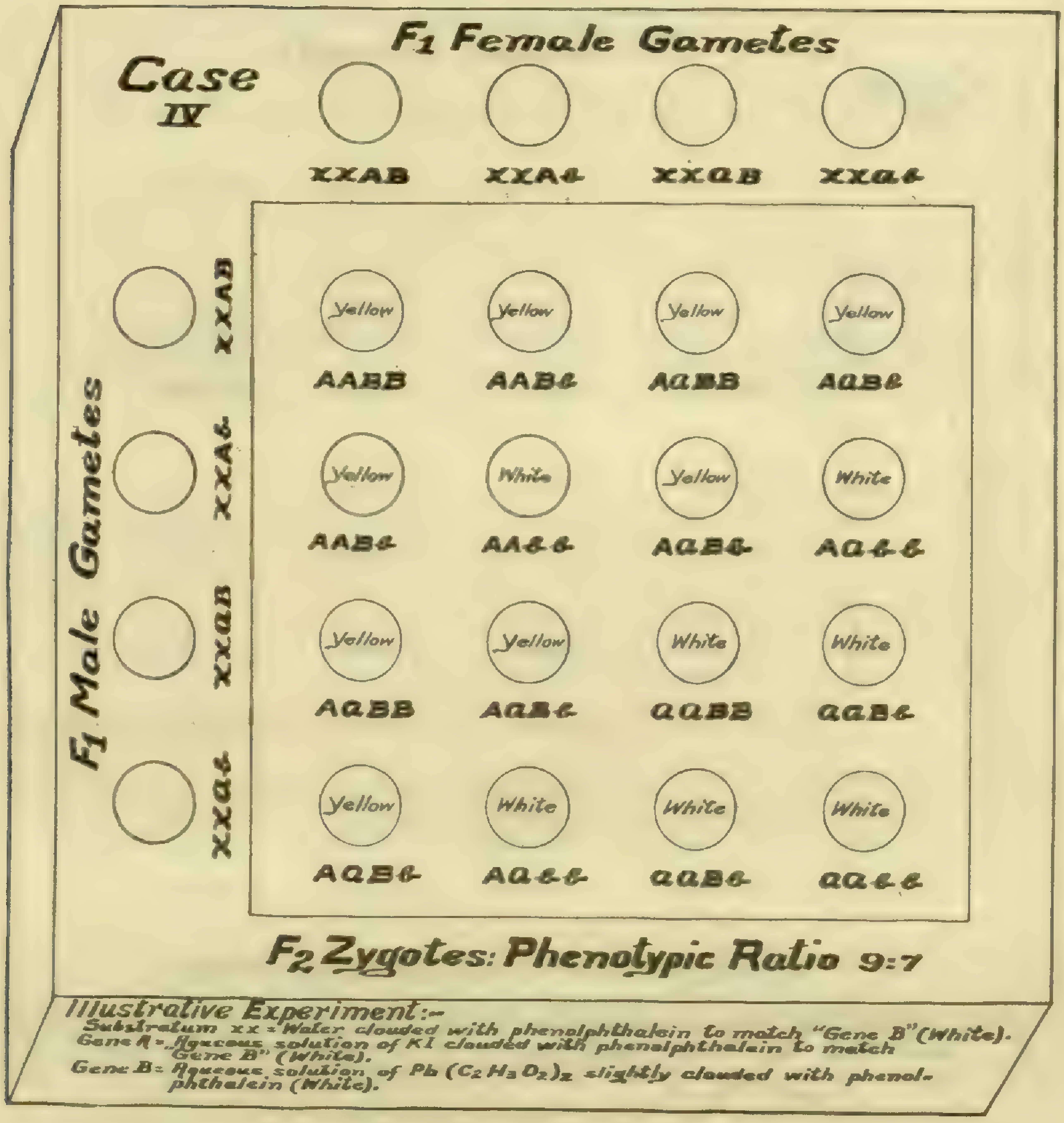
case may be. A word within a test-tube circle names the color of the reaction-product, which color is the index or analog of the somatic working out of its accompanying genetic formula of the soma.

Instructions for performing the experiment illustrative of each ratio-modification are found in detail in the drawing for the selected case. The chemicals representing gene "A" and gene "B" and the substratum are, as indicated, poured into the test-tubes representing the F_1 female and the F_1 male gametes. Each gamete-holding test-tube should contain approximately 20 c.c. of the appropriate genes and substratum. Of this mixture 4 c.c. represent 1 gamete; and 1 such gamete is to be poured into each one of the 4 zygote-holding test-tubes, directly below or directly to the right, as the case may be, of particular gamete-holding test-tube, following the checker-board method. Thus each of the 16 zygote test-tubes will contain chemicals appro-



priately representing 1 F_1 male and 1 F_1 female gamete free, like the constituents of a united sperm and egg, to interact in the zygote and in subsequent ontogenesis.

Some of these ratios, such as exist in Cases Nos. V, VI and IX, are much more difficult chemically to contrive than others, such as Nos. I, II, III, IV and X. It is not surprising, then, that nature provides more readily cases in inheritance representing the latter ratios, while the former are being found only by the most diligent genetical study. Not all of these ratios have yet been found in nature by experimental breeding, but, from time to time, a geneticist reports the discovery of a new di-hybrid F_2 ratio which proves to be a member of this series. Doubtless all of them will be found in time, but without introducing the special phenomena earlier referred to, Series A, consisting of 10 cases, exhausts the possibilities of F_2 phenotypic di-hybrid ratios.

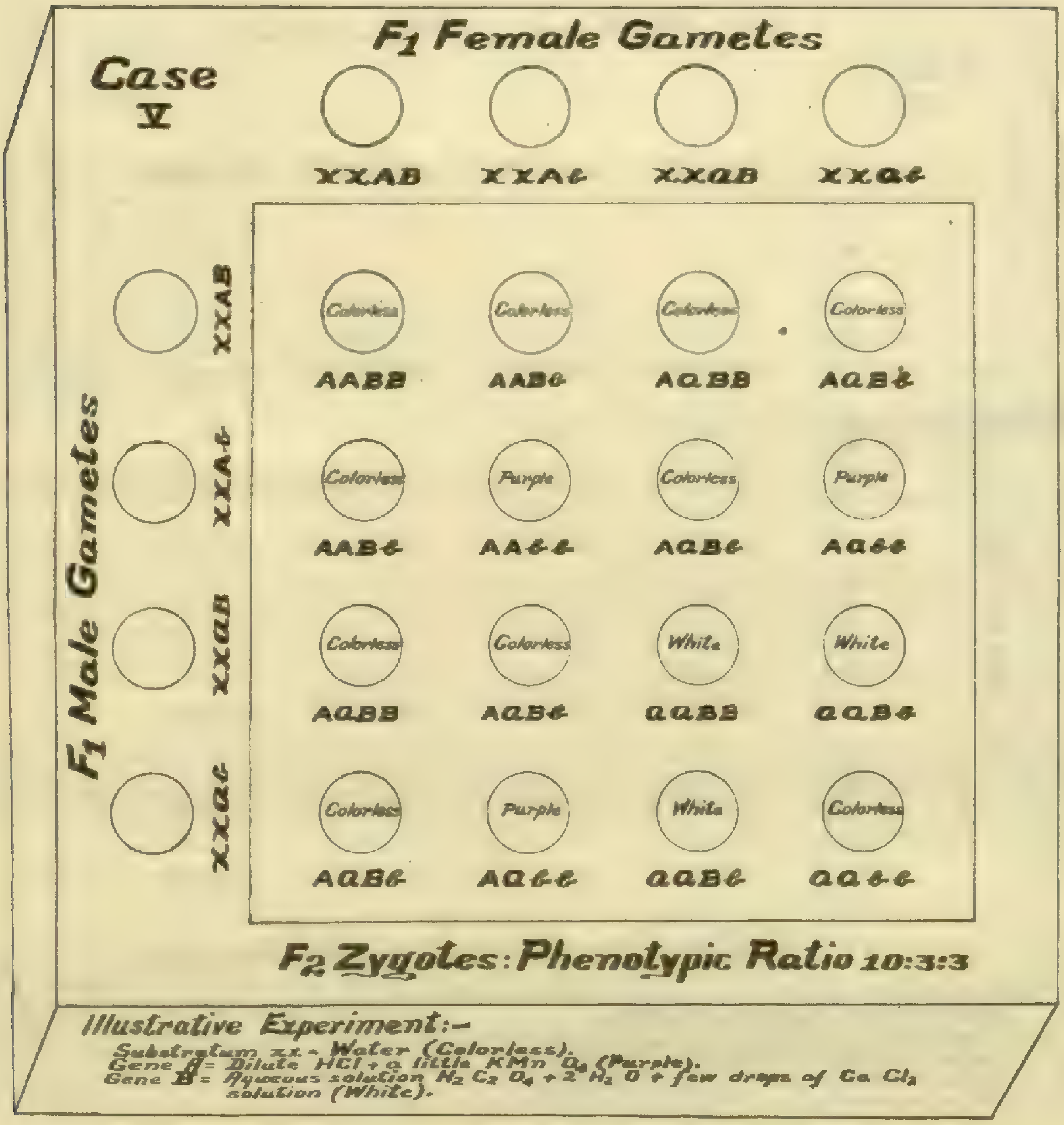


B. A CHEMICAL EXPERIMENT PARALLELING A MODIFICATION OF THE MENDELIAN F_2 DI-HYBRID PHENOTYPIC RATIO 1:2:1:-2:4:2:1:2:1 INVOLVING SOMATIC BLENDING AND GENIC SEGREGATION IN THE F_1 GENERATION

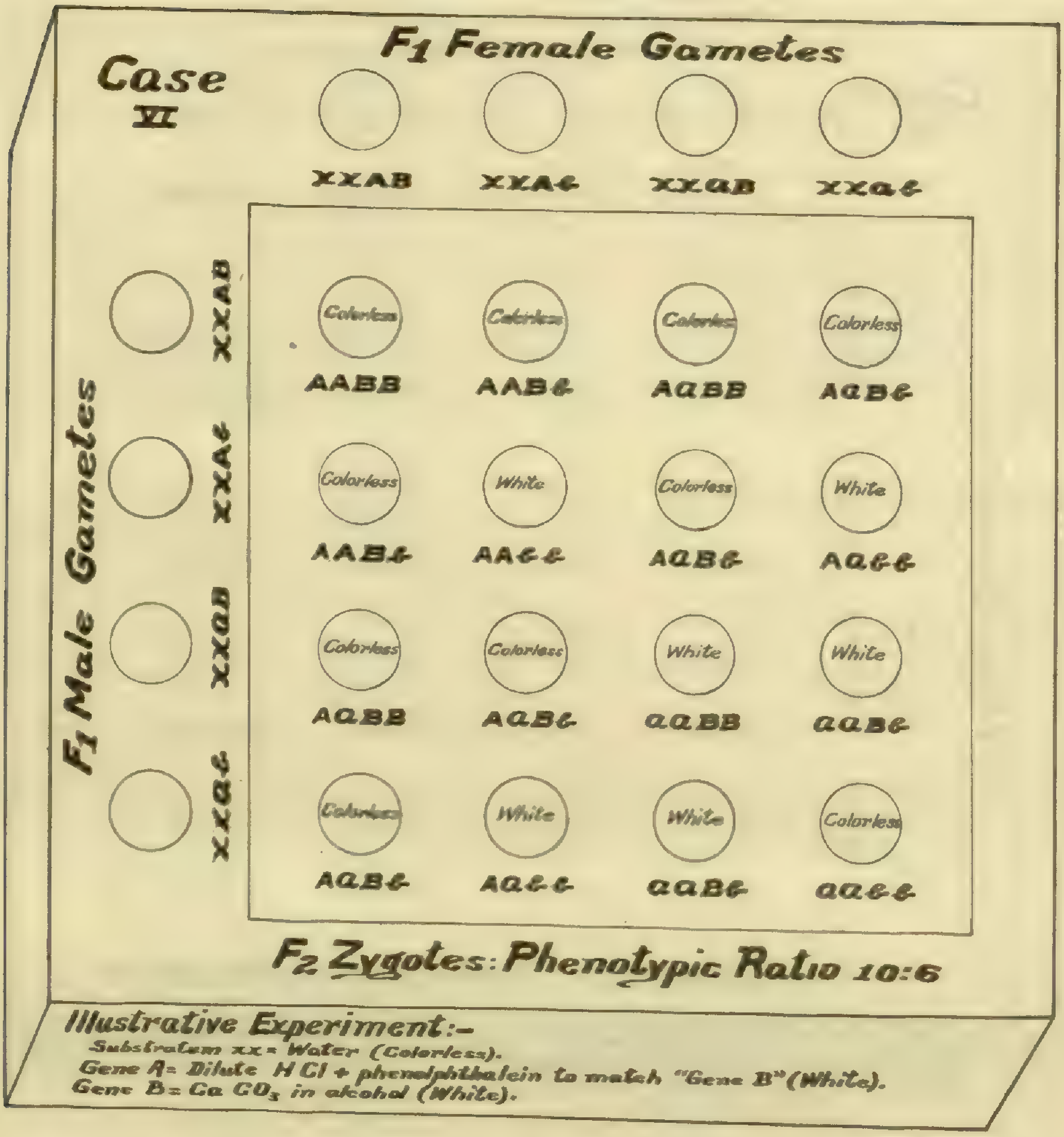
The ten cases described in the Series A are non-blending, in which the entities 9, 3, 3, and 1 are kept intact, that is, they are simply recombined. The mono-hybrid ratio on which they are based is the normal dominant-recessive 3:1 relation. The typical blending ratio in the F_2 mono-hybrid is 1:2:1. Carrying this latter ratio into the di-hybrid classification in the same manner as the 3:1 ratio was carried into the 9:3:3:1 classification gives us the following: 1:2:1:2:4:2:1:2:1, a total of sixteen individuals divided into 9 classes.

In Davenport's[3] study on the "Inheritance of Skin-Color in

[3] Davenport, C. B., "Skin-Color in Negro-White Crosses," Pub. 188 Car. Inst. Wash., 1913.

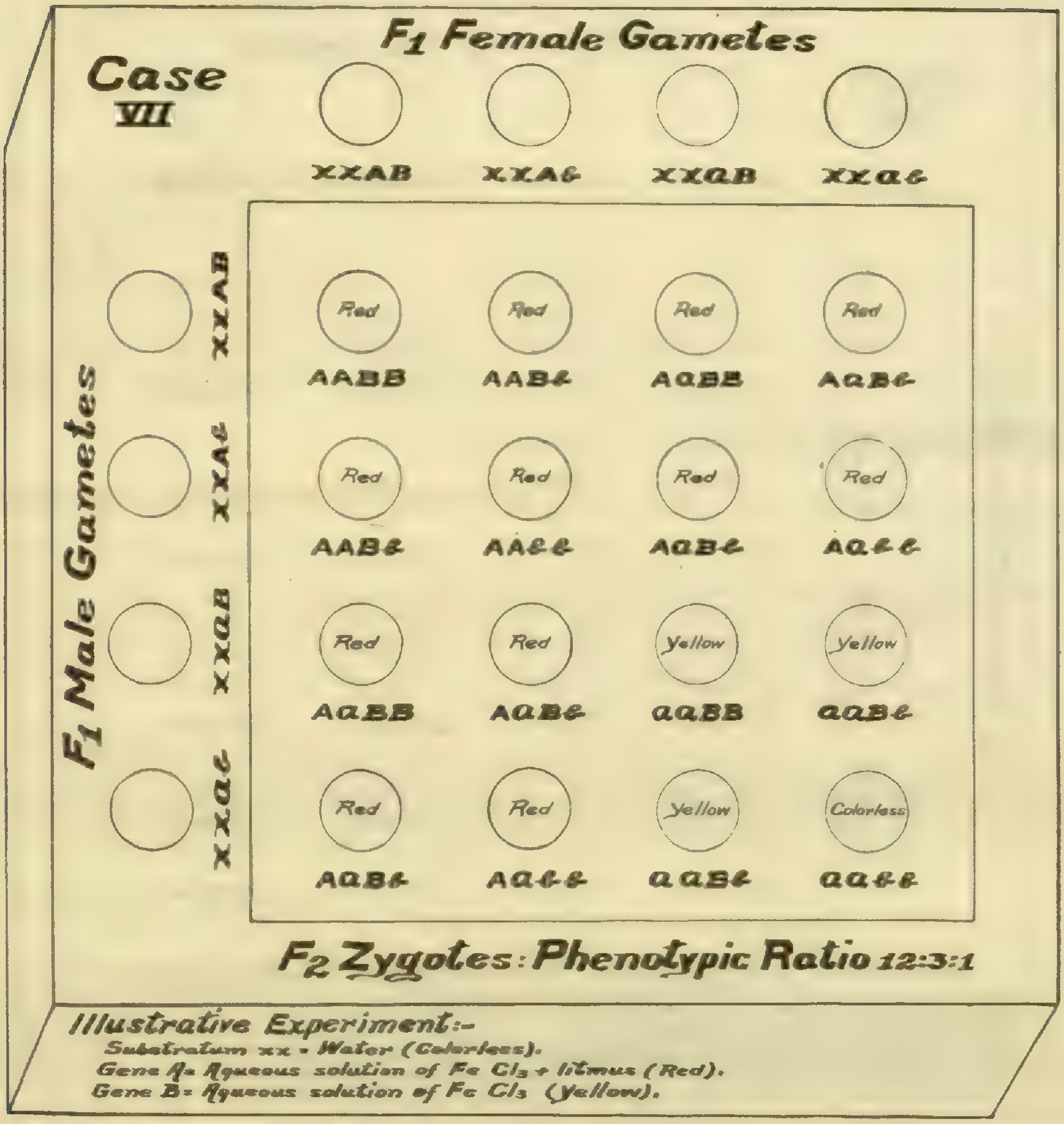


Negro-White Crosses'' he found that the amount of black skin-pigment in an individual is determined by two genes in each parental gamete, and in measuring the intensity of black skin-pigment in the members of a great many highly hybridized families he found 5 definite maxima in the curve plotting the distribution of individuals according to the per cent. of black skin-pigment carried. Theoretically (unless genes "A" and "B" are exactly equally potent in developing into a definite per cent. of blackness showing in the unweathered skin) there should have been 9 maxima in the above-described distribution curve. Arbitrarily giving the genes the following potentiality for somatic expression, "A" 16 per cent., "B" 19 per cent., "a" 1 per cent., "b" 2 per cent. (which is not far from the the facts of the case). the somatic frequencies and black skin-color percentages would run as follows: One 70 per cent., two 54 per cent., one 36 per cent., two 55 per cent., four 38 per cent.,



two 21 per cent., one 40 per cent., two 23 per cent., and one 6 per cent., in a total of 16 individuals.

But practically 5 instead of 9 somatic types were actually found because gene "A" and gene "B" are so nearly equal in value that it is not possible in a given individual, simply by measuring the skin-color pigment, to determine whether gene "A" or gene "B" is responsible for the quantity of melanin possessed. Thus in the 5 classes the two 54 per cent. cases (AABb) and the two 55 per cent. cases (AaBB) constitute the three quarters blacks or "sambos," the two 21 per cent. (Aabb) cases and the two 23 per cent. (aaBb) cases constitute the one quarter blacks or "quadroons," while the one 36 per cent. (AAbb) case and the one 40 per cent. (aaBB) case are so nearly like the four 38 per cent. (*i. e.*, the "mulatto" AaBb) that they constitute a single class of six individuals. Hence the contracted ratio 1:4:6:4:1.

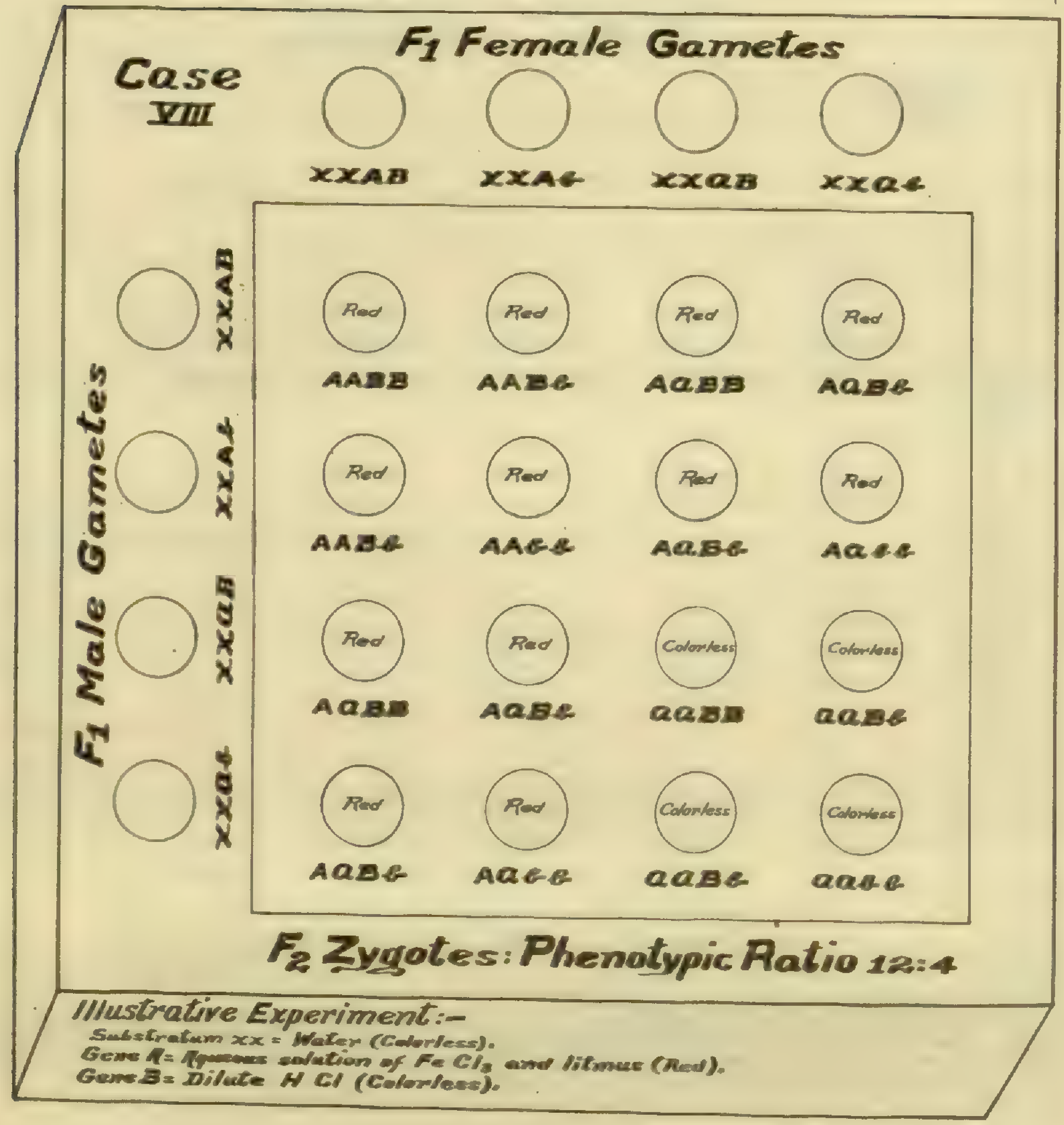


As Davenport clearly points out in the matter of black skin-pigment, each gene finds its definite somatic expression regardless of the presence of other genes. Since the two genes work out into the same somatic trait (*i. e.*, are duplicate genes) which somatic expressions differ only in quantity, they might well be be called cumulative genes. The accompanying diagram (Experiment Illustrative of Black Skin-Pigment Inheritance) gives specific directions for running this experiment in a manner very closely paralleling what Davenport found in nature.

This experiment illustrates only one case in a long possible series of modifications of the foundation F_2 di-hybrid phenotypic blending ratio 1:2:1:2:4:2:1:2:1.

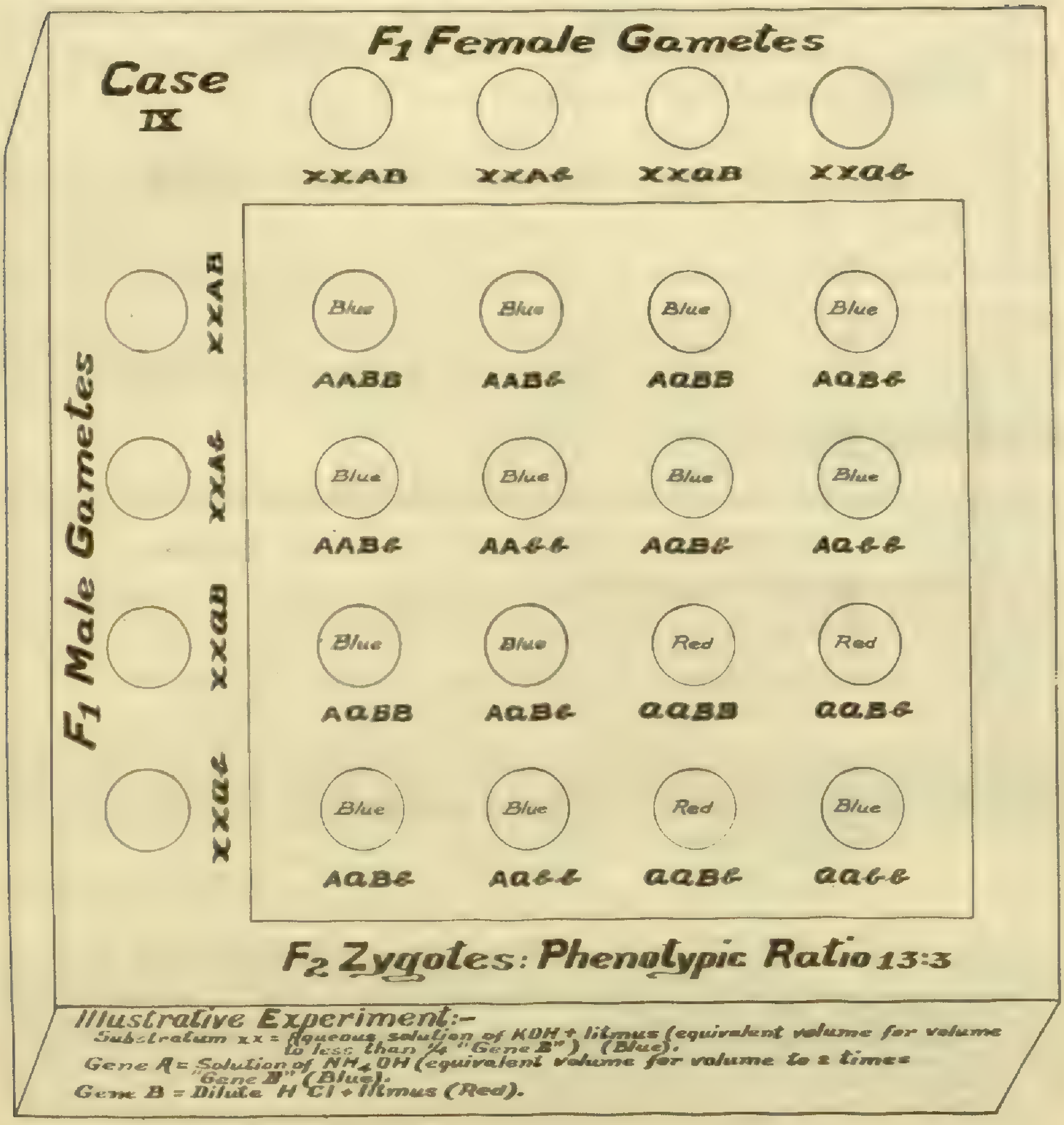
C. Other F_2 Di-Hybrid Series

In a case in which gene "A" does not blend with its allelomorphic mate "a" in the F_1 soma, but presents a typical case of

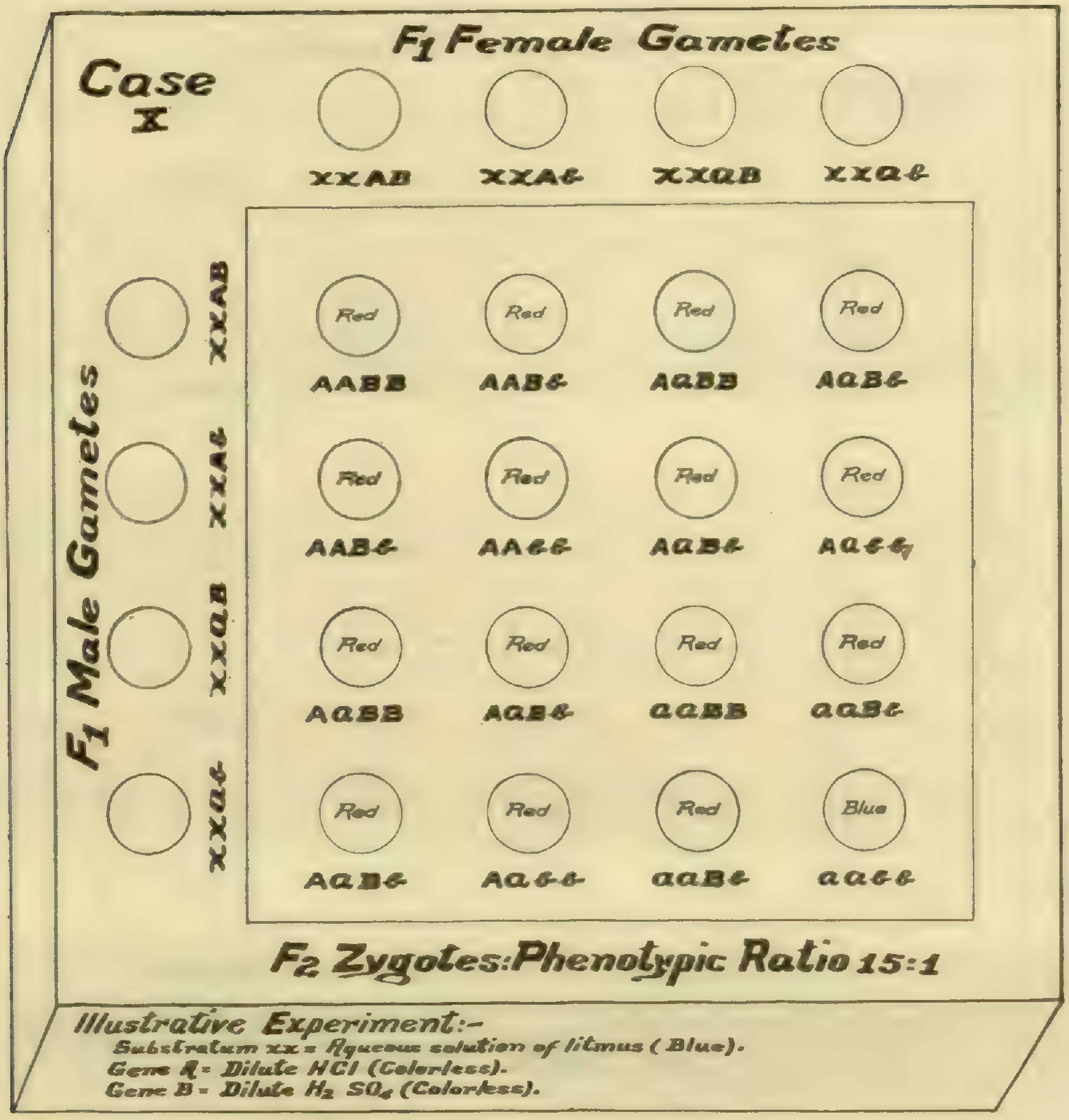


Mendelian dominance, while gene "B" blends with its mate "b" in the F_1 soma, the di-hybrid F_2 ratio resulting from combining two such trait-pairs is found by multiplying the F_2 mono-hybrid dominant relation $3+1$ by the F_2 mono-hybrid blending relation $1+2+1$, giving when expressed as a ratio the somatic F_2 di-hybrid relation $3:6:3:1:2:1$. Among other special cases to be considered are those involving crossing-over, non-disjunction and sex-limited inheritance.

When the genic and somatic specifications of a ratio are known it is not difficult to contrive a chemical parallel for it. The use of such experiments consists not only in clarifying the conception of the particular situation at hand, but also in providing in the laboratory a nearer approach than is usually used for demonstration to what is actually happening in heredity. The chemical analogy between what happens in the zygote-holding test-tube and what actually happens in the somatic working out of the



segregable genes in the members of the F_2 ratios is doubtless much closer than any completely mechanical contrivance can show. In the experiments the blending quite properly is shown complete in the zygote and soma, but if the analogy were carried still further one should be able to dip into the gamete-holding test-tubes and there find that some of the original F_1 genes remain unchanged—the unchanged germ-plasm which is left behind—and to lift out well-defined gametes with "A" or "a" and "B" or "b" variously combined, according to the constituent genes of the zygote, for in the living germ-cell cycle, not the blending of the soma, but clean-cut segregation is the rule. Representing the gametes by capsules containing genes in solid form, which capsules and genes would be slowly soluble in the substratum of the zygote, would drive the analogy a little closer to nature.



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COLD SPRING HARBOR H. H. LAUGHLIN.

THE FACTORS FOR YELLOW IN MICE AND NOTCH IN DROSOPHILA

IN a recent number of THE AMERICAN NATURALIST[1] appeared a paper by Ibsen and Steigleder on "Evidence for the Death in Utero of the Homozygous Yellow Mouse." In summing up (p. 751), after stating that "our evidence tends to confirm the conclusion of Castle and Little that in mice homozygous yellow zygotes are produced in the yellow × yellow mating, but that these

[1] Vol. LI, No. 612, December, 1917, pp. 740–752.

zygotes fail to develop normally after implantation in the uterus,'' they suggest ''that in mice there may be a 'lethal factor,' similar to those so well known in *Drosophila*, which is so closely linked to the factor for yellow that they are practically at the same locus and there is consequently no crossing-over.''

If the postulated factors are indeed so closely linked that crossing-over *never* occurs, would it not be simpler and even more logical to assume that but a single allelomorphic pair of factors is involved? Such an assumption necessitates a second, namely, that one of the factors of this pair is dominant in one of its expressions (yellow) and recessive in a second (lethal).

Morgan[2] has recently made a similar assumption for the mutant sex-linked factor in *Drosophila* which causes ''notch'' in the wings. He states that it is ''dominant in regard to the wing character but recessive in its lethal effect. A female with notch wings carries the gene in one of her X-chromosomes and the normal allelomorph in the other X-chromosome. Half of her sons get the former and die, the other half get the latter X-chromosome and live. As there are no lethal bearing males, the females must in every generation be bred to normal males.''

If Morgan is right in his assumption, there seems to be no reason, *a priori*, why factors having both dominant and recessive expressions should be limited to sex-chromosomes.

Stating that crossing-over has not been observed in a certain number of generations, even though the number of both individuals and generations is large, is, however, a very different matter from proving that crossing-over *never* occurs. Just where the evidence ceases to be negative and becomes positive, perhaps depends upon the ratio between the space occupied by a factor and the total length of the chromosome bearing it, in its relation to the law of probability, and to possible factors restricting crossing-over.

The data necessary for such a calculation does not appear to be available for either mice or *Drosophila*. Which interpretation is assumed must therefore for the present be a matter of personal preference. The continued failure to find crossing-over will in each case tend to make the one involving a single allelomorphic pair of factors more probable.

William A. Lippincott

Kansas State Agricultural College,
January, 1918

[2] Amer. Nat., Vol. LI, No. 609, September, 1917, pp. 513–544.

NOTES AND LITERATURE

Genetics in Relation to Agriculture. By E. B. Babcock and R. E. Clausen. New York: McGraw-Hill, 1918. Pp. ix–xx + 675, Fig. 239, Pl. 4.

Every geneticist who opens this volume in a spirit of hope and expectation will close it with appreciation and satisfaction, with a feeling that a tremendous task has been worthily accomplished. Unquestionably it will fill a real need as a text-book. In addition it should be of great service to the general biologist—using that term in its broadest sense—who wishes to have a compendium of genetical facts for ready reference.

The work is divided into three parts; it is really three volumes in one. In the first part the fundamental principles of genetics are outlined, in the second plant breeding is discussed, in the third animal breeding is considered.

There are thirty-nine chapters and an excellent glossary. The bibliography of twenty-four pages is not complete and does not purport to be complete. It is a list of the actual titles consulted in the preparation of the manuscript, truly no light undertaking.

The reputation of both authors as careful investigators is so firmly established that one is not surprised to find the immense volume of genetic literature of the past eighteeen years judiciously weighed and sifted, but that they found the time during the selection of material for so much constructive and illuminating criticism is perhaps not to have been anticipated. Moreover, since an investigator is not necessarily a good text-book writer, one suspects that the general excellence of the book from the pedagogical standpoint is due largely to Dr. Babcock's special training and long experience as a teacher.

After an introductory chapter on the methods and scope of genetics, the authors have chosen to open the volume by treating variation. Several modifications of older classifications of variation are given which may or may not prove useful. They were probably included rather tentatively as introductory to the main business of the chapter, the action of external stimuli in modifying development and causing germinal variation. Some of the illustrations here are not all that might be desired,

for example, the work of T. H. White on making new varieties of tomatoes by adding large quantities of fertilizers, which is rather hesitatingly cited. But perhaps one should criticize matter which does not appear rather than matter which does appear. In other words, if the reviewer may express his own hope in the connection, it is to see a more extended, well-rounded discussion of the action of the factors of environment in a later addition.

The statistical study of variation has been given a very pleasing treatment. The mathematician will undoubtedly complain that it is amateurish because it is given with a minimum of technical language. But just there lies its value in such a text-book. The necessary statistical tools are described so clearly that the elementary student can hardly err in their use. The more advanced student is properly directed elsewhere.

The physical basis of heredity is also discussed with great independence. The chromosome hypothesis is accepted without reservation. Cytological details not bearing directly on the subject in hand are not even mentioned, while those described—though accurate as far as they go—are somewhat diagrammatic. It will be interesting to see how this treatment works out in the classroom. No doubt many will find it a welcome change from the interminable details of unknown significance that often fill the pages of books on genetics. At the same time it is perhaps to be regretted that the difference between the higher plants and the higher animals in gametogenesis, and the bearing on genetics of the conflict between supporters of parasynapsis and telesynapsis, are not given more space.

A hundred and fifty pages are devoted to Mendelian interpretations of breeding facts. A wealth of illustration is used, and almost all types of Mendelian ratios are represented, although it is not easy to gather them together in a general *ensemble.* The older treatments of Plate and of Goldschmidt, where every theoretical modification of the Mendelian ratio was mentioned and then a case in point cited, had their value from a pedagogical standpoint, and it is rather to be deplored that their use was not continued. The newer data, in particular the work of Morgan and his students, is admirably presented, however. For the first time text-book treatment of crossing over, interference, and the various other phenomena discovered in *Drosophila,* is given in such a manner that the beginning student should be able to grasp the essential points without difficulty.

Interesting chapters on species hybridization, pure lines and

mutations comprise the remainder of part one. The discussion of mutations will probably not please DeVries, but it certainly is more in accord with all the facts than most other essays on the subject.

The applied genetics, animal breeding and plant breeding, filling twenty-four chapters, ought to be received with great approbation. Its compilation must have been very difficult, and its usefulness should be in direct proportion to the work involved. There is a great deal of new material of a strictly practical nature such as the origin of sweet pea varieties, breeding disease-resistant plants, etc. On the other hand, there is really no definite line to be drawn between part one and parts two and three. Theoretical genetics runs all through the book. For example one finds the treatment of heterosis, graft-hybrid chimeras and bud mutations in part two; and in part three discussions of Mendelian inheritance in domestic animals, acquired characters, non-Mendelian theories of sex-determination, the hormone theory, etc. The work is so well done that it must be read to be appreciated. The reviewer has but one suggestion to make concerning it, and this not in the nature of a criticism. Partially sterile hybrids between species, as is shown in Chapter 12, supply particularly useful material for the improvement of domestic animals and cultivated plants. If one studies carefully the history of domestic species, fragmentary as it is, he is astounded at the enormous number of cases in which the ancestry involves two or more species. Would it not be well to emphasize this point by extended illustrations in a book on plant and animal breeding?

The authors are to be congratulated on having brought together the material for a classical text-book on genetics. Revision will doubtless soon be necessary as is suggested in the preface. If it is made with the care that such an excellent foundation deserves the work will unquestionably go through many editions.

The McGraw-Hill Company deserve no little credit for the generous way in which they have seconded the authors' efforts. The typography, illustrations, paper and binding are extremely good. We understand that this is their first contribution toward a series of agricultural text-books under the general editorship of C. V. Piper. A standard has been set that is a good augury for the future.

E. M. E.

THE

AMERICAN NATURALIST

Vol. LII. August–September, 1918 Nos. 620–621

THE RELATION BETWEEN COLOR AND OTHER CHARACTERS IN CERTAIN AVENA CROSSES[1]

PROFESSOR H. H. LOVE and W. T. CRAIG

In Cooperation with the Office of Cereal Investigations, U. S. Department of Agriculture

Species crosses among oats have not been studied to any great extent, yet they offer some very interesting problems. Trabut[2] says:

> Hybridization between the cultivated species of oats has not yet been methodically attempted to my knowledge, and there is here a very interesting open field. It is true that we have yet to determine in what degree a true hybridization will be possible. If *Avena fatua sativa* may be crossed with *A. sterilis culta,* a progeny may be produced having very useful mixed characters. *A. abyssinica* will gain by being crossed with the really superior *A. strigosa.* But in the matter of hybridization there is much more to be gained from experimentation than from the mere discussion of theoretical views.

Since this paper was read (1911) some studies have been reported on with different species crosses in oats. Zade[3] discusses results obtained from a cross between *fatua* and *sativa.* He found F_1 to be intermediate and that the F_2 gave types resembling *fatua, sativa,* and the F_1 intermediate type. These with respect to awns and hairs gave a 1:2:1 ratio.

Surface[4] has described rather fully some results ob-

[1] Paper No. 70, Department of Plant Breeding, Cornell University, Ithaca, N. Y.

[2] *Journal of Heredity,* Vol. 5, pp. 84–85, 1914. (Translated from the original article published 1912.)

[3] Der Flughofer, *Deut. Landw. Gesell. Ab.,* 279: 1–91, 1912.

[4] *Genetics,* Vol. 1, No. 3, pp. 252–286, May, 1916.

tained from a cross between *Avena fatua* × *Avena sativa* var. Kherson. The two parent forms differ in a number of characters some of which may be given here. The *Avena fatua* is brown or black in color, has both kernels awned and pubescent and has the typical wild type of base surrounded by a tuft of basal hairs. The Kherson is yellow in color, has few or no awns and lacks pubescence on the glumes and has the typical *sativa* base on which is found an occasional hair.

The F_1 type is intermediate between the two parents. The color of grain is brown but somewhat lighter than the wild parent, and the larger kernel in the spikelet is usually awned,[5] while the smaller or upper kernel is never awned. The lower grain exhibits a medium pubescence while the upper grain is always smooth. The base is intermediate between the two parent forms with tufts of hair on each side but not all around the base.

Some of the results of the F_2 generation may be given in Surface's conclusion:

> The data show that the wild parents carry genes for gray and probably for yellow color in addition to the black. These three colors seggregate independently of each other. The observed ratio closely approximates the expected and confirms Nilsson-Ehle's conclusions.
>
> The cultivated base of the grain is dominant to the wild and segregates independently of the color genes. The heterozygous condition in the lower grain can be recognized in the majority of plants.
>
> In this cross seven pairs of characters are completely correlated with the character of the base. The characters associated with the wild base are (1) heavy awn on the lower grain, (2) awns on the upper grain, (3) wild base on the upper grain, (4) pubescence on the pedicel on the lower, and (5) on the upper grain, (6) pubescence on all sides of the base of the lower grain and (7) pubescence on the base of the upper grain.
>
> The gene for pubescence on the back of the lower grain is partially linked with the black color factor. The F_2 generation is too small to determine the exact degree of linkage but indicates that there are about 0.7 per cent. of crossovers.

[5] Surface, on page 258 of *Genetics*, Vol. 1, No. 3, 1916, says, "the majority of the lower grains show a weak, straight awn" and on page 265 says "the majority of F_1 spikelets show no awn whatever." It is not clear just which is meant.

The gene for pubescence on the back of the upper grain segregates independently of the color factor except that in the absence of the gene for pubescence on the lower grain the gene for pubescence on the upper is unable to act. In this sense the gene for pubesence on the lower grain is a basic pubescence factor similar to the color factor (C) found in many animals and plants.

Material and Methods

The present authors have been working with oat species crosses for several years. A number of different combinations have been made and studied, including several species and many of their derivatives. It is planned here to emphasize certain results obtained with a cross between *Avena fatua* and *Avena sativa* var. Sixty Day. This Sixty Day variety is identical with the Kherson as used by Surface so far as general varietal characteristics are concerned, yet no doubt there are many strains of both sorts.

The *Avena fatua* in appearance was similar to the type used by Surface and has the characters described above. The Sixty Day oat is yellow and seldom do any awns appear. There are no dorsal hairs but an occasional basal hair may be found.

The plants used in making these crosses were grown in the greenhouse since a greater number of successful pollinations can be made than when the plants are grown in the field. The *Avena fatua* was used as the female parent and a number of flowers were emasculated and pollinated. Three seeds developed and each produced a plant. The F_1 generation plants were also grown in the greenhouse since they may receive greater care and more seed may be obtained. All later generations were grown in the field, spacing the plants two to three inches in the rows.

Discussion of Results

The F_1 type was as described by Surface, generally intermediate in type. The color was brown somewhat lighter than the wild type. The large kernel of the spikelet was often awned and was covered with dorsal

hairs. The small kernel of the spikelet was never awned but had an occasional sprinkling of dorsal hairs. The base was more like the *sativa* type, yet appeared to be more intermediate in type with some basal hairs on either side of the base but not at the back.

When the seeds from the first generation plants were sown, a number of different types appeared in the second generation. There were some that resembled the two parent forms and also other types different in color, amount of awning, pubescence, and the like.

As regards color there appeared four types, black, gray, yellow and white. The white ones, of which there were only four, were tested later and proved to be gray, thus leaving only the three color types. The black oats were of two general types, those having the two strong awns and pubescence on both kernels and the wild base, and those having pubescence on the large kernel and sometimes on the small one and with an intermediate or *sativa* type of base. Some of these forms were awnless and others possessed varying amounts of awn which were in some cases strong and in others weak.

The gray colored oats were both pubescent and smooth, some fully awned, some partially awned, and some awnless. They also segregated as to type of base.

The yellow oats, however, were all smooth and possessed very few or no awns. No yellow oats developed the strong awns similar to the wild type.

The segregation as to color and percentage of awns of the second generation plants is shown in Table I.

TABLE I

Showing the Segregation as to Color and Percentage of Awns. Series 687, *Avena fatua* × *Avena sativa* var. Sixty Day

Percentage of Awns

Color	0	1–9	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100	Totals
Black	46	25	20	23	12	17	21	23	14	8	2	99	310
Gray	11	9	6	10	3	10	6	5	1	3		28	92
Yellow	9	7	1	1									18
Totals	66	41	27	34	15	27	27	28	15	11	2	127	420

The percentage of awns was determined by taking a typical head from each plant and counting the total number of spikelets and the number of awned spikelets, and then determining the percentage of awned spikelets. Since there are a number of plants having no awns and also a number having 100 per cent. it seems best to arrange the classes as has been done in this table; that is, separate classes have been made for the 0 and 100 per cent. values.

From this table it is clear that the black oats possessed varying degrees of the awned condition from awnless to fully awned. The grays too showed about the same range of distribution. The yellow types, however, showed a tendency to be grouped in the lower classes. No yellow types were found having more than 30 per cent. of awns. It seems quite evident that there may be some relation between the yellow oat and the lack of awning.

Nilsson-Ehle[6] has discussed a case of a cross in oats where there was an apparent inhibition of awning produced by a yellow oat. He concludes that there was some inhibitory effect of the yellow color or that the yellow color factor acted also as an inhibitor of awns. The oats Nilsson-Ehle worked with were domestic types and it is a well-known fact that the domestic sorts vary as to the amount of awns with the change in environment. For that reason it is felt that results obtained from wild crosses will be more definite since the wild type produces its fully awned condition under very diverse growth conditions. This is all the more evident from a cross of this same Sixty Day type used in these crosses with a black cultivated oat. It was found that the yellow oats segregating from this cross contained fewer awns than did the blacks, whites, and grays but that the percentage of awns on the black parent was so variable that the results obtained are not definite. Such is not the case for the awning of the *Avena fatua* as stated above.

[6] *Zeitschrift für induktive Abstammungs- und Vererbungslehre*, Bd. XII, Heft 1, 1914.

These results show that the segregation as to color, as mentioned above, produces three types, black, gray and yellow. On the assumption that the wild oat carries genes for black, gray and yellow we would expect a segregation of 12 black : 3 gray : 1 yellow. These figures approach this result, but there are too few yellows and too many grays. Instead of the numbers obtained we expect 315.00 blacks : 78.75 grays : 26.25 yellows. It is very difficult to always distinguish between pale grays, yellows and whites, a fact which is well known to those working with oats. This is especially true in unfavorable seasons when oats are likely to weather badly. No doubt this difficulty is one of the reasons for the deviation of the gray and yellow classes. When we group the non-blacks together we have a very fair approximation to the 3 : 1 ratio, which ratio would be expected on the above assumption.

The relation between color and pubescence for these same second generation plants is well illustrated by Table II.

TABLE II

SHOWING THE RELATION BETWEEN COLOR AND PUBESCENCE OF THE SECOND GENERATION PLANTS OF SERIES 687, *Avena fatua* × *Avena sativa* VAR. SIXTY DAY

Pubescence

Color	Both Kernels Pubescent	One Kernel Pubescent	Smooth	Totals
Black	112	198		310
Gray	26	42	24	92
Yellow			18	18
Totals	138	240	42	420

Certain interesting facts are brought out by this table. It is apparent that all of the black oats are pubescent, some having both kernels pubescent and a larger number having only the one kernel pubescent. It is very significant that there are no smooth black oats. The gray oats, on the other hand, have a certain number of which both kernels are pubescent, a larger number with one

kernel pubescent, and still another lot of smooth oats. It seems that the gray oats segregate as to pubescence on what may be a 1:2:1 ratio. Regarding the yellow oat it is very significant that all of them are in the smooth class. That is, no yellow oats are found which are pubescent. Certain ones which were found appeared yellow but which proved on testing to be gray instead of yellow, so that at present no true yellow oats which are pubescent have been obtained out of this cross.

From these data it seems without any doubt that yellow oats in some way or another tend to inhibit the factor for pubescent. It is also apparent that there is one factor for pubescence which is linked with the black color factor. There sems to be another factor for pubescence which is independent of any color factor and for this reason we obtain gray oats in approximately the ratio of 1:2:1 so far as pubescence is concerned. Owing to the inhibiting effect of the yellow oat, there are no pubescent forms obtained. From this material it is clear then that we are working with a *fatua* form which has two factors for pubescence, one of which is linked with the black color factor and one which is independent. More will be said regarding these facts later in this paper, when another cross will be mentioned.

Another interesting relationship is that shown between the color in the F_2 generation and the segregation as to type of base. As mentioned earlier in this paper, the type of base differs from the wild form which is the typical sucker-mouth shape while that of the cultivated oat is of the typical *sativa* form. The *sativa*-like form is dominant or partially so to the wild type. A study of this and a large number of other crosses in which the wild type has been used as one of the parents indicates that the segregation of the base follows the 1:3 ratio, wild being the recessive type.

The relation between color and type of base for the second generation plants of this cross is shown in Table III.

TABLE III

SHOWING THE SEGREGATION AS TO COLOR AND TYPE OF BASE. SERIES 687. *Aventa fatua* × *Avena sativa* VAR. SIXTY DAY

Type of Base

Color	Wild	Sativa	Totals
Black	97	213	310
Gray	26	66	92
Yellow		18	18
Totals	123	297	420

From this table it is clear that the black oats segregates into the wild and *sativa* forms as also do the grays. On the other hand, the yellow oats exhibit no wild type of base but are all of the *sativa* class. It is also apparent from these data, then, that in addition to the inhibition of awn production and pubescence there is also some factor or factors which inhibit the production of the wild type of base when this particular cross is made. That it must be due to some factor or factors related to the yellow oats is clear from the fact that with a large number of crosses in which white oats and other forms have been used, the grays and whites as well as the blacks exhibit the wild type of base in about the ratio that would be expected.

TABLE IV

SHOWING THE RELATION BETWEEN COLOR AND PERCENTAGE OF AWNS FOR THE THIRD GENERATION FAMILIES PRODUCED FROM THREE HETEROZYGOUS PLANTS OF THE SECOND GENERATION. SERIES 687. *Avena fatua* × *Avena sativa* VAR. SIXTY DAY

Percentage of Awns

Color	0	1–9	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100	Totals
Black	82	45	17	9	3	4	5	3	4			58	230
Gray	12	13	6	1	2	1	2	1		1		18	57
Yellow	10	7	2			1	1						21
Totals	104	65	25	10	5	6	8	4	4	1		76	308

Seed from a large number of F_2 plants were tested in the F_3 generation but all of these will not be discussed here. Three of these which exhibited the segregation

similar to that obtained in the F_2 generation have been brought together and the results are here shown for the three classifications made on the second generation.

The relation between color and percentage of awns of these three families mentioned above is shown in Table IV.

Here again, it is apparent that the black oats ranged all the way from awnless to 100 per cent. awns as do the gray oats. The yellow oats, on the other hand, are grouped near the lower percentage classes. Two individuals, however, exhibited about 50 per cent. of awns, one being in class 40 to 49, one in 50 to 59. It may be that these will be found to be grays instead of yellows. However, in general, the tendency is for the yellows to exhibit only a few awns. This is in accordance with the results obtained on the second generation and substantiates the conclusion drawn from the study of that material. It may be worth while to call attention here to the segregation as to color which fits the hypothesis more closely than does the material of the second generation. The segregation exhibits what is without doubt a 12:3:1 ratio. The observed numbers are 230 black: 57 gray: 21 yellows while the expected numbers are 231.00 blacks : 57.75 grays : 19.25 yellows.

The relation between color and pubescence on these third generation families is shown by Table V.

TABLE V

SHOWING THE SEGREGATION AS TO COLOR AND PUBESCENCE OF THREE F_3 FAMILIES GROWN FROM HETEROZYGOUS F_2 PLANTS. SERIES 687

Pubescence

Color	Both Kernels Pubescent	One Kernel Pubescent	Smooth	Totals
Black	91	139	—	230
Gray	19	12	26	57
Yellow	—	5	16	21
Totals	110	156	42	308

Here it is clear that again all the black oats are pubescent while the gray oats fall into the three classes. The

segregation of the grays does not follow the 1:2:1 ratio here but it is possible that some of those classed as non-pubescent may have a few hairs when examined more closely. It was found with the second generation material that it was necessary to use a lens with certain ones, especially where there was very little pubescence showing. This has not been done with all those in this table and, therefore, it is possible on later examination that some of them may fall into the group of one kernel pubescent. The yellow oats also, instead of all being in the non-pubescent group, have a few in the class having one kernel pubescent. It is likely that on later examination these will be found to be gray oats. This can not be said at present. In general, it may be said that this segregation agrees very closely with that of the second generation with the exception of the five yellow plants which seem to exhibit some slight amount of pubescence.

The relations between color and type of base for these same three third generation families is shown in Table VI.

TABLE VI

SHOWING THE RELATION BETWEEN COLOR AND TYPE OF BASE IN THREE THIRD GENERATION FAMILIES. SERIES 687, *Avena fatua* × *Avena sativa* VAR. SIXTY DAY

Type of Base

Color	Wild	Sativa	Totals
Black	57	173	230
Gray	18	39	57
Yellow		21	21
Totals	75	233	308

On examining this table it is clear that the segregation of these third generation families agrees very closely with that of the second generation material. The black and gray oats have both wild and *sativa* bases in apparently a 1:3 ratio. The yellow oats, on the other hand, have only the *sativa* base. This material tends to substantiate the conclusions drawn from the second generation material, which is to the effect that it does not seem

possible to produce a yellow oat from this cross having the type of base of the wild parent.

Further information may be had regarding pubescence and color on examining the results on three other third generation families which have been grouped according to color and pubescence. The parent plants which produced these three families were black, pubescent on one kernel and nearly awnless.

These results are shown in Table VII.

TABLE VII

SHOWING THE RELATION BETWEEN COLOR AND PUBESCENCE FROM THREE THIRD GENERATION FAMILIES OF SERIES 687, *Avena fatua* × *Avena sativa* VAR. SIXTY DAY

Pubescence

Color	One Kernel Pubescent	Smooth	Totals
Black	231		231
Yellow		88	88
Totals	231	88	319

The segregation shows that no gray was present and that the segregation is only for blacks and yellows so far as color is concerned and follows an approximate 3:1 ratio. In regard to the pubescence it is clear that all of the black oats are pubescent while all the non-blacks or yellows are smooth. This material further substantiates the statement made earlier in this discussion to the effect that there is a pubescent factor linked with the black oat.

GENERAL DISCUSSION

The foregoing data show that there is a very definite relation between color of glume and production of awns. On the black and gray oats awns are produced in varying amounts while few or no awns are produced on the yellow oats. Regarding the inheritance of awns, it has been shown[7] that the weak awn is inherited on a 1:3 ratio, the fully awned condition being recessive. The data

[7] Love, H. H., and Fraser, A. C., "The Inheritance of the Weak Awn in Certain Avena Crosses," AMER. NAT., 51, No. 608, August, 1917.

that have already been collected show also that the strong awn is inherited in the same manner. These data (Tables I and IV) give 203 fully awned : 525 partially awned or awnless, giving 2.92 : 1.12 per 4. We would expect on a 1 : 3 basis 182 : 546. The action of the yellow factor is to reduce the amount of awns on the yellow glumed oats.

It was stated earlier that there was apparently a pubescence factor linked with the black and also another pubescence factor which was not linked with any color. If this were true and there was no inhibitory effect produced by the yellow oats we would expect to obtain 15 pubescent to 1 non-pubescent form in the second generation. It may be well to state here that it has been found by experiment that the wild form used in this cross was of such a type that it had two factors for pubescence. We have also found another form which has only one factor for pubescence. When this form is crossed with a white oat, all of the non-blacks are smooth, showing that this form has the pubescence factor which is linked with the black while the forms having the two factors for pubescence give both pubescent and smooth non-blacks. This is well brought out by the data presented in Table VIII. Here the same white sort, Tartar King, was crossed with two forms of *Avena fatua*.

This table is made up of data of the second generation. It is possible that later experimentation may change the relationship of the colors particularly so far as the grays and whites are concerned. In these tables all those not showing blacks and grays are classed as yellows and whites. The further study of these has not proceeded far enough to determine just the relation here. It seems, without doubt, that we have two types of *fatua*, one giving the 15 : 1 ratio (Series 351a1) and one the 3 : 1 (Series 351b1). Again in the 3 : 1 distribution all the non-blacks are smooth.

It will be of interest here also to state when the type having one factor for pubescence was crossed with the Sixty Day type similar to the one used in Series 687 that all of the non-blacks, both grays and yellows, were

TABLE VIII

SHOWING THE SEGREGATION AS TO COLOR AND PUBESCENCE ON A CROSS BETWEEN *Avena fatua* and *Avena sativa*, VAR. TARTAR KING

Series 351a1 — *Pubescence*

Color	Both Kernels Pubescent	One Kernel Pubescent	Smooth	Totals
Black	30	74		104
Gray	9	19	3	31
White and yellow	3	3	5	11
Totals	42	96	8	146
	138		8	

Series 351b1 — *Pubescence*

Color	Both Kernels Pubescent	One Kernel Pubescent	Smooth	Totals
Black	72	144		216
Gray			61	61
White and yellow			18	18
Totals	72	144	79	295
	216		79	

smooth, showing that this form has the pubescence factor closely linked with the black color gene.

The results as obtained from Series 687 so far as color and pubescence are concerned may be explained in the following manner. We may assume the *Avena fatua* to be represented by BBGGYYPP, that is, possessing the factors black (B) which also produces pubescence, gray (G), yellow (Y) and another factor (P) for pubescence. The Sixty Day oat then may be bbggYYpp. We then assume Y to inhibit the production of pubescence in the absence of B or G.

It may also be well to state that the results here found can also be explained by assuming Y to have the effect of producing pubescence in the presence of G. We would then not assume any pubescence factor (P) for this explanation. This assumption would account for the results as well as the one chosen. On the other hand, from data already obtained on other crosses it does not

seem that this latter explanation is the one which should be used.

On the first hypothesis the F_1 individuals are, therefore, BbGgYYPp forming eight kinds of gametes. From this assumption then we would expect 48 black pubescent : 9 gray pubescent : 3 gray smooth : 4 yellow smooth. The ratio of pubescent to non-pubescent would be 57 : 7. The observed numbers in the second generation were 378 pubescent : 42 smooth. We would expect 374.06 pubescent : 45.94 smooth. The observed numbers from the three third generation families gave 266 pubescent : 42 smooth, while we would expect 274.31 : 33.69. Considering the two groups together we have 644 pubescent : 84 smooth, while we would expect 648,375 : 79.625. We see that the observed facts agree very well with the theory.

While it is not intended to go into details regarding the F_3 generation, it may be said that a number of observed facts tend to substantiate this hypothesis. For example, we should have some families segregating in the third generation giving 15 pubescent : 1 smooth. This we find to be so. Again we would, according to theory, expect to find some F_3 families segregating into blacks and grays where the grays would all be smooth. This we find also. We would also expect some gray oats to segregate into 9 pubescent : 7 smooth. This combination has also been found.

Regarding the base, it might be well to state that in studying the segregation of this series into the third and even into the fourth generation as yet no yellow oat has been found exhibiting the wild type of base. These results do not agree with those obtained by Surface although in general we might expect them to be similar since the yellow Sixty Day oat and the Kherson type are classed by some as the same variety of oat. Yet when we know that it is possible to obtain different strains out of a variety, particularly so far as the inheritance is concerned, it is not surprising that these results should not agree. Let us illustrate this by some results we have

obtained from crossing two black oats which by those studying classification of varieties of oats have been classed as the same variety and exhibit the same general botanical characters. When these two forms were crossed, both being black, the first generation plants were black but when the second generation was grown it was found that a segregation was obtained, giving 15 black to 1 non-black. This point then illustrates the statement made above that we shall probably obtain different segregations even though we are supposed to be using the same variety. This is also brought out by the fact that from the wild form, *Avena fatua,* we have been able to obtain different types so far as pubescence is concerned. How many other types may exist in the wild form of *fatua* we do not know, but experiments are underway to determine whether it is not possible to find other types as regards color and certain other characteristics.

From what is here said we do not intend to convey the idea that yellow color as found in oats will inhibit the production of awns, pubescence and base but mean merely that the yellow as exhibited in this series does that. In fact, we know from the crosses we have already studied where other yellow forms have been used that it is possible to obtain the yellow pubescent form and yellow ones with the wild base. Therefore, the statements made here hold only for the particular cross here reported.

Conclusion

The studies here presented show that we have some relation between these yellow oats and the absence of awns, pubescence, and the wild base. We also find that there are two types of pubescence, or better stated, two factors for pubescence, one of which is linked with black and one which is independent of any color factor. Owing to the inhibitory effect, we do not get a definite Mendelian ratio from these studies. It is also clear that the third generation material tends to substantiate the conclusion arrived at from the study of the second generation plants.

STUDIES IN PALEOPATHOLOGY.

III. Opisthotonus and Allied Phenomena among Fossil Vertebrates

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Every student of the fossil vertebrates who is fortunate enough to collect a number of complete or approximately complete skeletons of fossil vertebrates is almost sure to be impressed with the frequency of the peculiar curve to the backwardly bent neck and the rigid appearance of the limbs, if these members are preserved in anything like the position assumed by the animal at death. This attitude of the skeleton is very common in the petrified remains of extinct animals and it is doubtless what is known to medical men as opisthotonos. Williston[1] in describing the remains of *Cimoliosaurus Snowii*, a long-necked plesiosaur, from the Cretaceous of Kansas, says:

> The specimen comprises the skull and twenty-eight cervical vertebræ, all attached and with their relative positions but little disturbed. They lie upon the right side, with the usual opisthotonic curve to the neck, and are all laterally compressed.

The attitude has been noted among many other fossil vertebrates, but its significance, so far as I am aware, has never been commented upon.

Many of the beautifully complete skeletons of the small pterodactyls (Fig. 1), *Pterodactylus longirostris, P. brevirostris, P. elegans*, from the lithographic slate of Aichstädt, which were described many years ago by Goldfuss, Cuvier, Wagner and Soemmering, exhibit a marked opisthotonic curve to the neck and a more rigid appearance to the skeleton as a whole than is common among the skeletons of these remarkable vertebrates. *Pterodactylus*

[1] *Trans. Kansas Acad. Sci.*, 1890, p. 1.

longirostris Cuvier has the jaw gaping as if trismus was not an accompaniment of opisthotonos, such as is usually the case in recent times, or else the jaw was secondarily moved by the action of the water after the dissolution of

FIG. 1. *Pterodactylus micronyx* H. v. Meyer from the lithographic slates of Eichstädt in Bavaria. The original is in the paleontological collections at Munich. This specimen shows a typical opisthotonic position. One half natural size. After Broili.

the muscles. Other pterodactyls, such as *Pterodactylus scolopaciceps, P. longicollum,* and others described by Plieninger[2] from the Jura of Swabia show no indication of any spastic distress.

The toothed bird (Fig. 2), *Archeopteryx macroura,* from the lithographic slates, commonly figured in the textbooks of geology, zoology, and paleontology, exhibits a pronounced opisthotonos, which may be slightly exaggerated in all the slender-necked vertebrates having a relatively heavy head. The weight of the head may have added to the curve, but the position is none the less a genuine opisthotonos. The skeleton of a small dinosaur.

[2] *Paleontographica,* Bd. LIII, pp. 210–313, 6 Tafeln, 1907.

FIG. 2. *Archaeopteryx macroura* from the lithographic slates, showing a typical opisthotonos. × ¼.

about the size of the modern turkey, described and figured by Hoernes as *Compsognathus longipes* Wagn. (Fig. 3) from the lithographic slate of Kelheim, exhibits an unusually well-developed opisthotonos, the skull lying far back over the pelvis.

Probably the most complete representation of opisthotonos among fossil vertebrates is that seen in the skeleton of the small cursorial dinosaur, *Struthiomimus altus*

(Fig. 4) described by Osborn[3] from the Belly River series. The skeleton of this interesting dinosaur is mounted in a panel mount where the skeletal parts are placed approximately as found (Fig. 4). The attitude is typically opisthotonos, the jaws exhibiting trismus, with the head

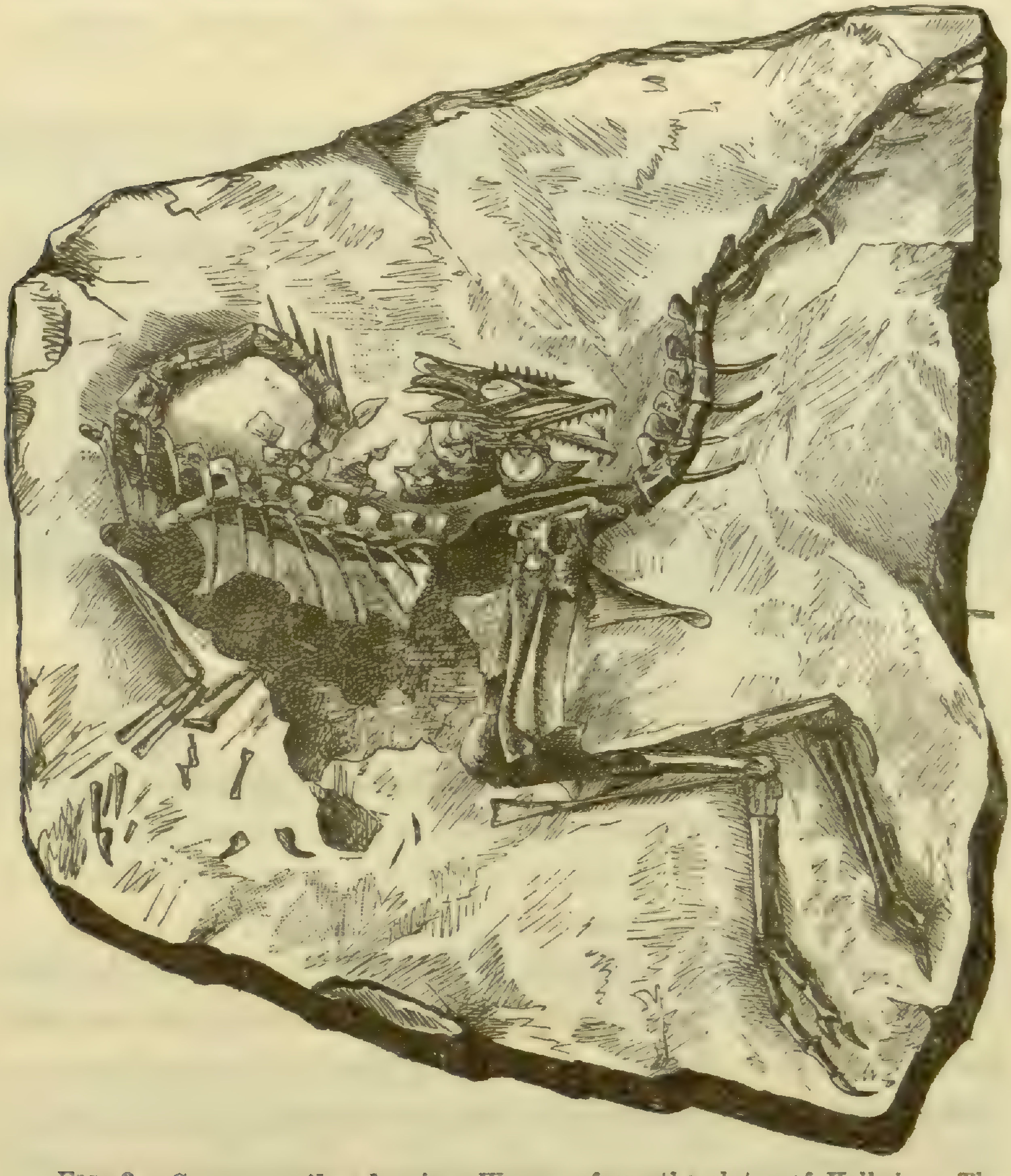

FIG. 3. *Compsognathus longipes* Wagner, from the slates of Kelheim. The position of the head and tail are characteristic expressions of a tetanic spasm. After Hoernes.

thrown sharply back over the sacrum, the tail thrown sharply up; the toes strongly contracted, with the

[3] Osborn, H. F., 1917, "Skeletal Adaptations of *Ornitholestes, Struthiomimus, Tyrannosaurus*," *Bull. of the Amer. Mus. Nat. Hist.*, Vol. 35, pp. 733–771, Pl. XXIV.

phalanges closely appressed. The whole attitude of the body strongly suggests some severe spastic distress. The animal may have been a plant feeder and its death and spastic distress due to feeding on some poisonous plant, such as to-day causes tetanic spasms in animals. It may have suffered death from a severe cerebrospinal infection, but whatever the cause of its death, the attitude of the

FIG. 4. Skeleton of *Struthiomimus altus*. Genotype specimen, Amer. Mus. 5339. 1/30 natural size. In this panel mount the animal is placed approximately as found. The attitude is typically opisthotonos. After Osborn.

animal strongly suggests the effect of disease, and in discussing the history of disease among animals the opisthotonic position exhibited by fossil skeletons must be considered as indicating a possible diseased condition.

The correlative phenomenon, pleurothotonos, is less common among the higher vertebrates, but is not uncommon among the fishes. This is evidently the attitude assumed by the skeleton of the plesiosaur, *Plesiosaurus macrocephalus* (Fig. 5), collected by Miss Mary Anning from the Lias of Lyme Regis, England, and figured by William Buckland in his "Bridgewater Treatise."[4] It is improbable that the head of this long-necked plesiosaur could have been turned into its present attitude by a current of water, since a force sufficiently strong to have moved the heavy head to one side would doubtless have

[4] Vol. II, Pl. 19, Fig. 1, 1837.

disturbed other portions of the body, and there is no evidence of this in the skeleton.

The remarkable specimen of *Geosaurus gracilis* H. von Meyer, from the upper Jurassic lithographic slate of Eichstädt, Bavaria, as described and illustrated by von Ammon, shows a clearly marked instance of pleurotho-

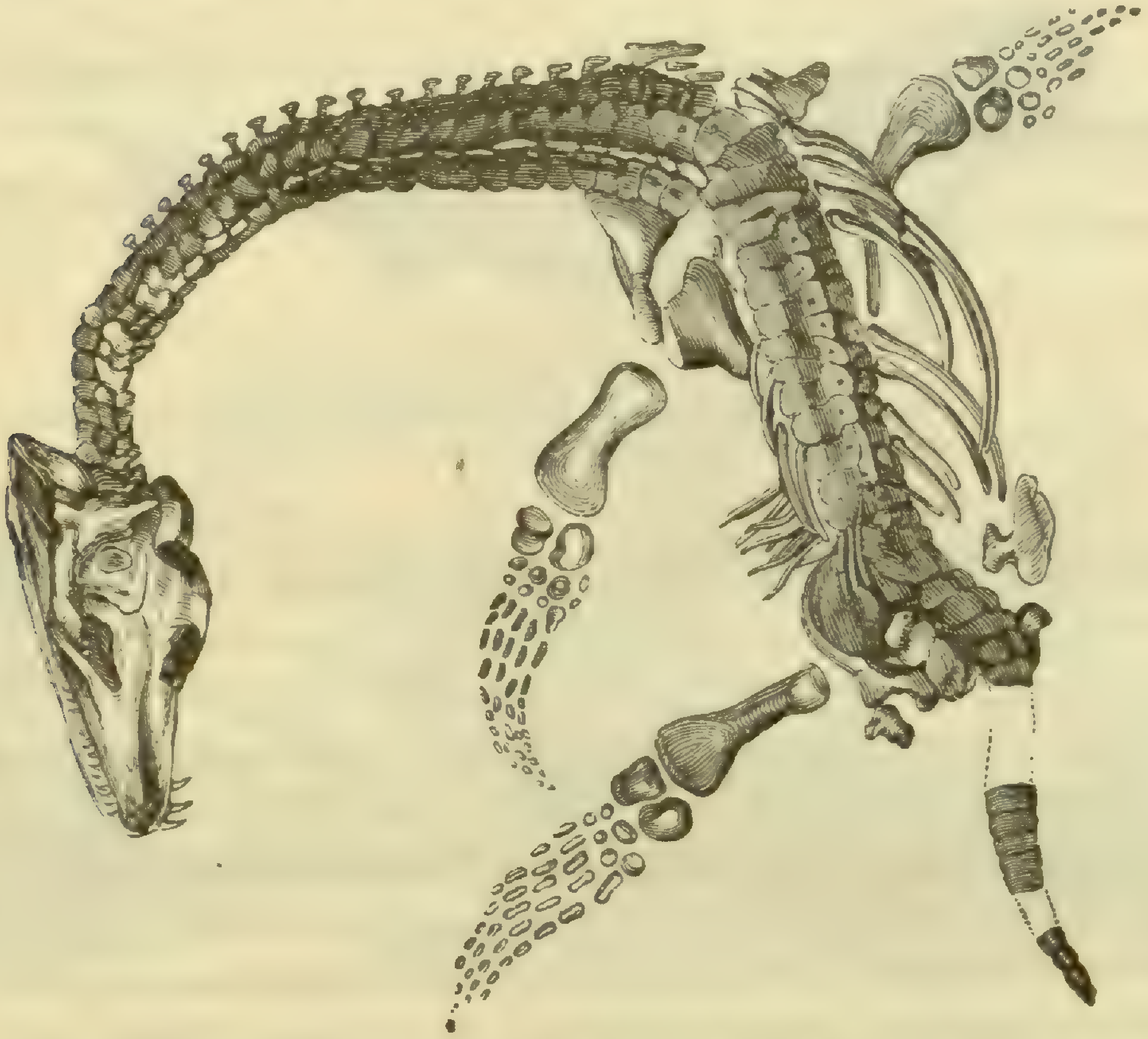

FIG. 5. *Plesiosaurus macrocephalus*, a skeleton from the Lias of England, preserved in a pleurothotonic attitude. After Buckland.

tonos. The body, slightly twisted, is bent into a strong, uniform arch toward the left, the animal having been preserved on its belly.

The fishes often assume at death and are fossilized in the pleurothotonic attitude. This is clearly indicated in the fishes from the Solenhofen, *Leptolepis sprattiformis*, as figured by Dreverman, Gaudry and others, though this attitude is also clearly that of fishes attempting to flop out of the soft mud back into the water. It is not a necessary sequence that all laterally compressed verte-

brates assume the pleurothotonic attitude, since often the ganoid fishes (Fig. 6), especially, assume the opisthotonos. It is true that the majority of fishes which are preserved in an approximately complete manner exhibit no trace of either of these attitudes. The great series of Triassic fishes from Connecticut seldom exhibit indica-

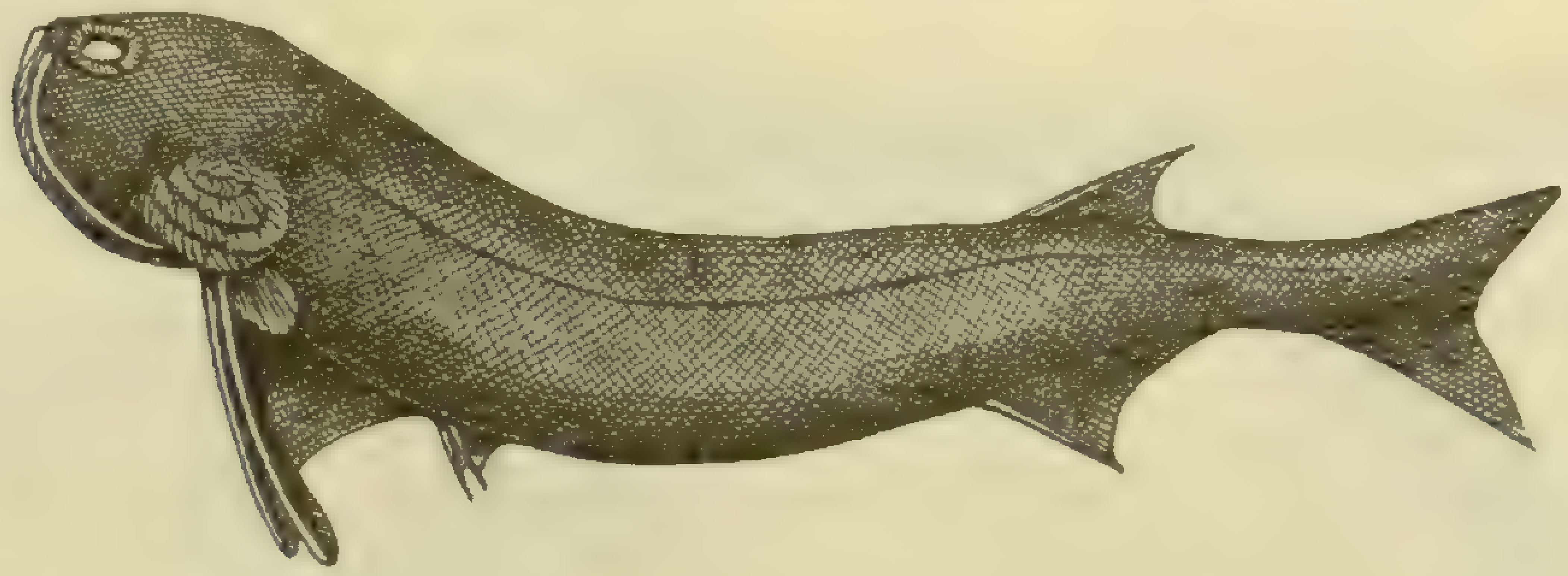

Fig. 6. *Acanthodes gracilis* F. Roemer, a ganoid fish from the Permian of Klein-Neundorf, Lower Silesia, showing an opisthotonic position. After Hoernes. Hoernes.

tions of either of these phenomena. A single specimen of *Catopterus gracilis*, of those figured by Eastman,[5] exhibits the opisthotonos, and a single one, *Ptycholepis marshi*, exhibits pleurothotonos. Of the scores of specimens of these fishes described by Newberry and Eastman a very small percentage show any sign of spastic distress.

As a clinical manifestation of great severity, opisthotonos and the correlative phenomena, pleurothotonos and emprosthotonos (episthotonos), have long been well known in human beings as accompanying certain phases of tetanus, abscesses of the brain, otitis media, hysteria, cerebrospinal meningitis, strychnine poisoning, and other afflictions, in which toxins affecting the nervous system are liberated. In these manifestations the muscles of the body, the spine and the extremities are strongly flexed. This characteristic attitude of the spasm has been graphically figured (Fig. 7) by Sir Charles Bell in his "Anatomy of the Expressions," where he says:

> I have here given a sketch of the true Opisthotonos, where it is seen that all the muscles are rigidly contracted, the more powerful flexors

[5] Bulletin 18, State of Connecticut, State Geol. and Natl. Hist. Survey, Pl. IX.

prevailing over the extensors. Were the painter to represent every circumstance faithfully, the effect might be too painful, and something must be left to his taste and imagination.

Opisthotonos has also been described by Falls[6] as occurring in the fetus in utero, the cause for which is still unknown.

It is a matter of great interest to find these same manifestations represented in the fossilized skeletons of ancient vertebrates. The majority of the attitudes assumed by the fossils may be due to the spasm usually incident to death, the *Todeskampf* of the Germans, or to acci-

FIG. 7. Charles Bell's drawing of a man in opisthotonos.

dental shifting after death. Many of the vertebrates whose skeletons are found in anything like a complete state of preservation do not show these manifestations. It is on the whole unusual for fossil vertebrates to show opisthotonos and much more common in the slender-necked species. It is possible that the animals whose skeletons are preserved in the above-mentioned attitudes had suffered death owing to diseases similar to tetanus, cerebrospinal meningitis, or similar disturbances.

The skeleton of *Mesosaurus brasiliensis* from the

[6] Surgery, Gynecology and Obstetrics, January, 1917, pp. 65–67.

Permian of Brazil[7] exhibits a slight degree of opisthotonos (Fig. 8) such as is common in the death struggle of many modern vertebrates. There can be, I think, little doubt that many of the opisthotonic attitudes assumed by fossil vertebrates are easily explained as a phenomenon accompanying the "Todeskampf," but whether all can be so

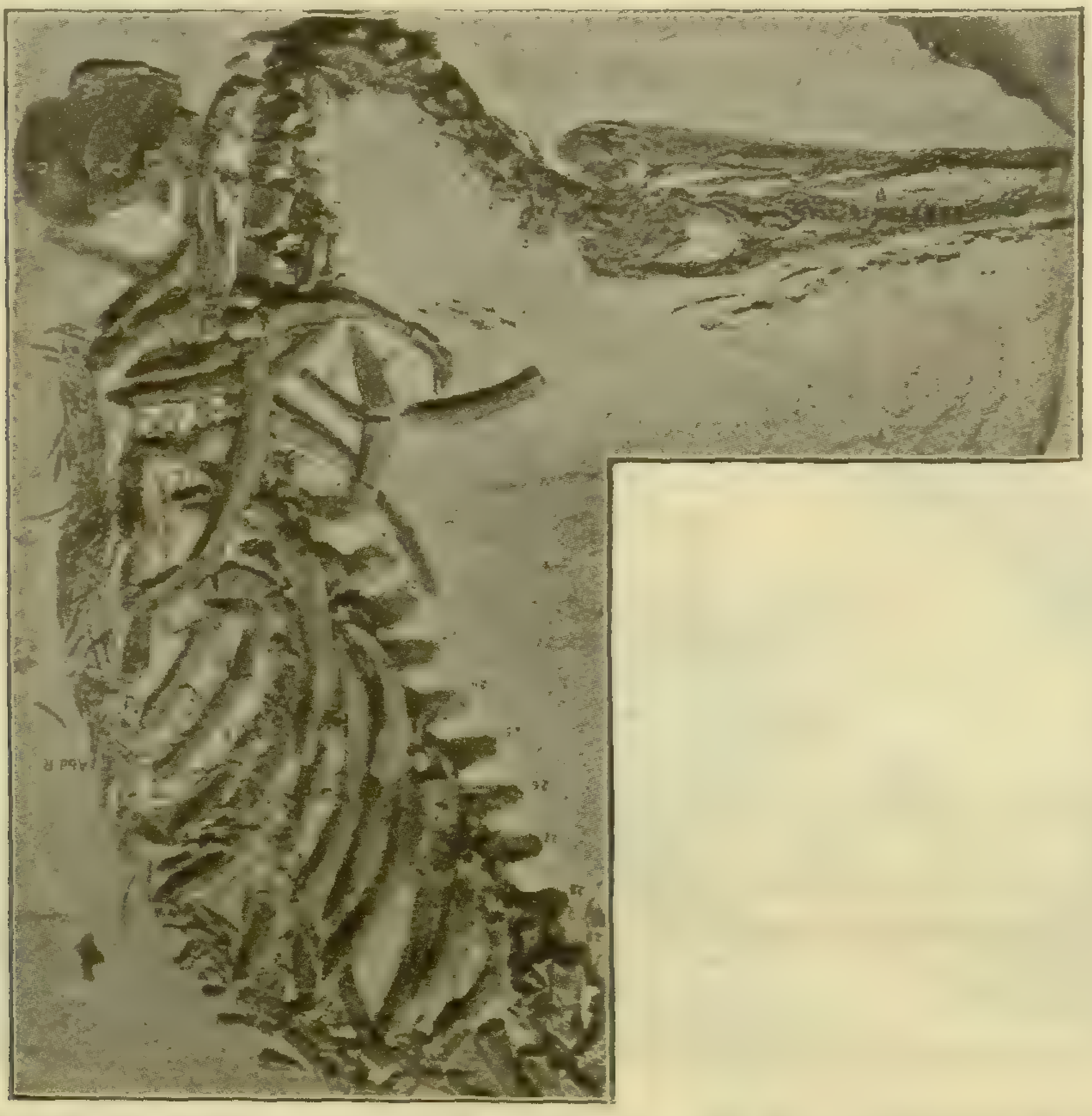

FIG. 8. *Mesosaurus brasiliensis* McGregor from the Permian of Brazil, showing a slight opisthotonos. After McGregor.

explained on this basis is extremely doubtful. It is certainly not true that all vertebrates exhibit indications of such spasms. While complete skeletal remains of fossil vertebrates are relatively rare, yet there is a sufficient number preserved which have been described to determine the relative frequency of these positions.

In the many complete skeletons of fossil reptiles from the Eocene of France described by L. Lortet[8] only four,

[7] McGregor, J. H., 1908, "Commissao de Estudos das Mines, etc.," Pl. IV.

[8] L. Lortet, 1892, "Les Reptiles du Bassin du Rhône," Archives du Museum d'Histoire Naturelle de Lyon, Tome V, pp. 3–139, Pl. I–XII.

Alligatorium Meyeri (Pl. X), two specimens of *Alligatorellus Beaumonti* (Pl. XI), and *Crocodileimus robustus* (Pl. IX), exhibit any degree of the opisthotonic attitude. Only one, *Pleurosaurus Goldfussi* (Pl. VII), exhibits the pleurothotonos. The majority of the remaining skeletons figured show no spastic distress whatever. So that while we may say that these two positions are common they are rather the unusual than the usual state of affairs.

On the other hand the dinosaurs *Struthiomimus altus* and *Compsognathus longipes,* many specimens of small pterodactyls and the fossil bird *Archeopteryx* exhibit such a marked opisthotonic attitude as to lead one to infer some cerebral-spinal or other intracranial infection which would have been easily possible in the poorly protected brain case of these early vertebrates. It requires but a glance at the nature of the brain case of the early vertebrates to see how poorly protected the cerebrospinal spaces were. Ingress of infecting bacteria may have been through any of the numerous nerve or vascular foramina, through the thin cancellous walls separating the brain case from the sphenoidal sinus, and through the anterior end of the brain case which was often protected only by a membranous covering, by cartilage, or by very thin bony plates.

The possible presence of the infecting bacteria has been so well established by the investigations of Walcott,[9] van Tieghem and Renault,[10] that little need be said here concerning them. Walcott has described and figured bacteria from fossilized Pre-cambrian algæ of central Montana, supposedly *Micrococcus,* the bacteria being arranged in groupings characteristic of the *Staphylococcus* isolated from a case of Pemphigus neonatorum by Falls.

[9] Walcott, C. D., 1915, "Discovery of Algonkian Bacteria," *Proc. Natl. Acad. Sci.,* Vol. 1, p. 258. Figs. 2 and 3; 1914, "Pre-Cambrian Algonkian Algal Flora," *Smith. Misc. Coll.,* Vol. 64, No. 2 (Publication 2271).

[10] Renault, B., 1900, "Microorganismes des combustibles fossiles." Bulletin de la Société de l'Industrie minerale Saint-Etienne, Serie III, 1899, Tome 13, pp. 865–1161; 14 (1–2), pp. 5–159, 1900, with Atlas, 1898–1899, Pl. X–XXV, Atlas, 1900–01, Pl. I–V.

by whose courtesy a photograph has been used for comparison. Renault has described a great variety of bacteria, many of which are apparently similar to the bacteria of to-day.

In searching for evidences of disease among fossil vertebrates I have been interested in making the above comparisons. In the light of the above study it seems probable that some of the instances of opisthotonos and pleurothotonos among fossil vertebrates may be due to acute cerebrospinal infections, the petrified skeletons exhibiting trismus, rigidity of the limbs, and the peculiar backward curvature of the vertebral column so common to-day as clinical manifestations of spastic distress. This is especially probable in the cases where the skeletons exhibit such marked opisthotonos and pleurothotonos as do many of the specimens above referred to. It may then be said that opisthotonos as seen in the skeletons of fossil vertebrates indicates disease only in those exaggerated cases of spastic distress as is evidenced by the attitudes assumed by fossil vertebrates, such as the small dinosaur, *Struthiomimus altus*, and the bird, *Archæopteryx macroura*. Not all vertebrates preserved in opisthotonus were victims of disease, but many of them suggest a strong neuro-toxic condition.

CANCER'S PLACE IN GENERAL BIOLOGY

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The condition which has been called cancer by the laity and the medical profession has been studied by the latter largely from the standpoint of disease. Investigators have considered its great destructive action, cause, prevention and treatment, all of which study has been stimulated by the urgent necessity of its eradication from the ills of man, and not in its relation to the known biologic facts concerning the universal conflict between living normal cells and their natural enemies. In order to approach correctly this biologic phase of the condition it will be necessary to answer the question: What is cancer?

To the pathologist, cancer is a cellular overgrowth which occurs in some multicellular organism, especially in man, and which is characterized by its apparently unlimited proliferation, during which it destroys tissues, and is fatal eventually to the whole organism. This, in general, is the conception held by the members of the medical profession, but to the scientific mind which is interested in and trained in the fundamental or more specific factors operating in living nature, it is neither satisfactory nor sufficient.

An analysis of the condition from such a biologic point of view necessitates also for its elucidation a study of the facts relative to the evolution of multicellular organisms from single cells as units of life. Biologists agree that the cell is the visible unit of life, and that all cells have certain fundamental structural and functional characteristics which are common to all. They further agree that all multicellular beings evolve by a process of division or segmentation of a single cell which has been stimulated automatically, or by the process of extrinsic fertilization to such activity.

During the process of segmentation certain dominant facts present themselves. A fertilized ovum, for exam-

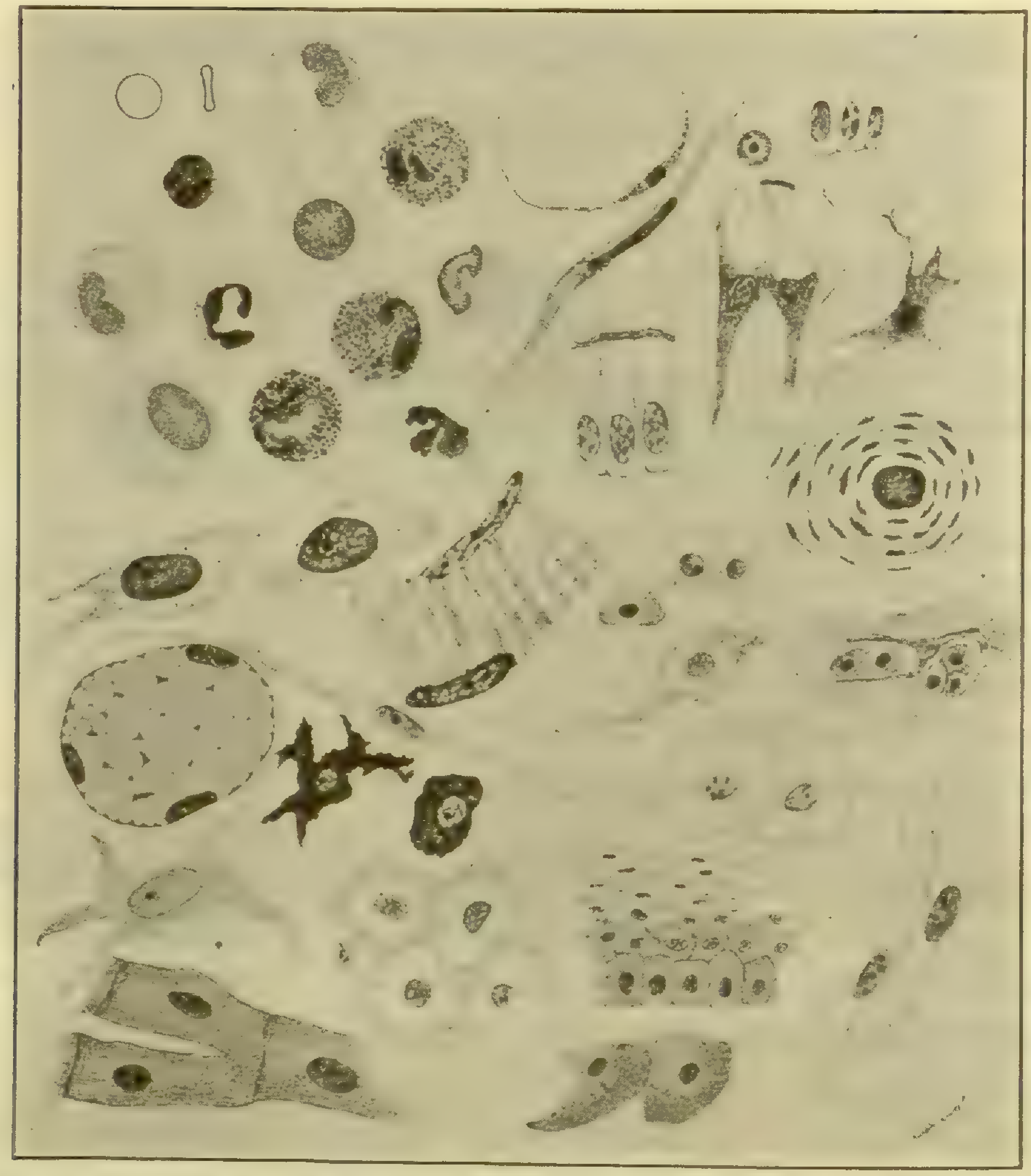

FIG. 1. Some of the differentiated cells (textocytes) of the human body:

Biologic Terminology	*Medical Terminology*
1. Erythrocytes,	Red blood corpuscles.
2. Lymphocytes (small),	Lymphocytes (small).
3. Lymphocytes (large),	Lymphocytes (large).
4. Transitional forms,	Transitional forms.
5. Leukocytes,	Polymorphonuclear leukocytes.
6. Eosinocytes,	Eosinophiles.
7. Mastocytes,	Mast cells.
8. Fibrocytes,	Fibrous connective tissue cells.
9. Rhabdomyocytes,	Striated muscle cells.
10. Melanocytes,	Pigmented cells.
11. Myxocytes,	Muscle cells.
12. Cardiomyocytes,	Heart muscle cells.
13. Lipocytes,	Fat cells.
14. Leiomyocytes,	Smooth muscle cells.
15, 18, 19. Adenocytes,	Glandular epithelium.
16, 24. Neurocytes,	Nerve cells (neurones).
17. Osteocytes,	Bone cells.
20. Endotheliocytes,	Endothelial cells.
21. Chondrocytes,	Cartilage cells.
22. Epitheliocytes,	Epithelial cells.
23. Tendocytes,	Tendon cells.
25. Sudorocytes,	Sweat cells.
26. Sebocytes,	Sebaceous cells.
27. Gustocytes,	Taste cells (of a taste bud).

ple, divides; the cellular divisions divide; these continue to divide and form eventually, in a definite period, the millions of cells which constitute the organism. This is a simple statement of general facts, but coincidentally with these facts there is an orderly sequence of cellular changes which seems to be foreordained in the original fertilized ovum; the cellular progeny does not retain, to the same degree, all of the structural and functional characteristics of the original cell (ovocyte). There is a grouping of cells which is coincident with morphological

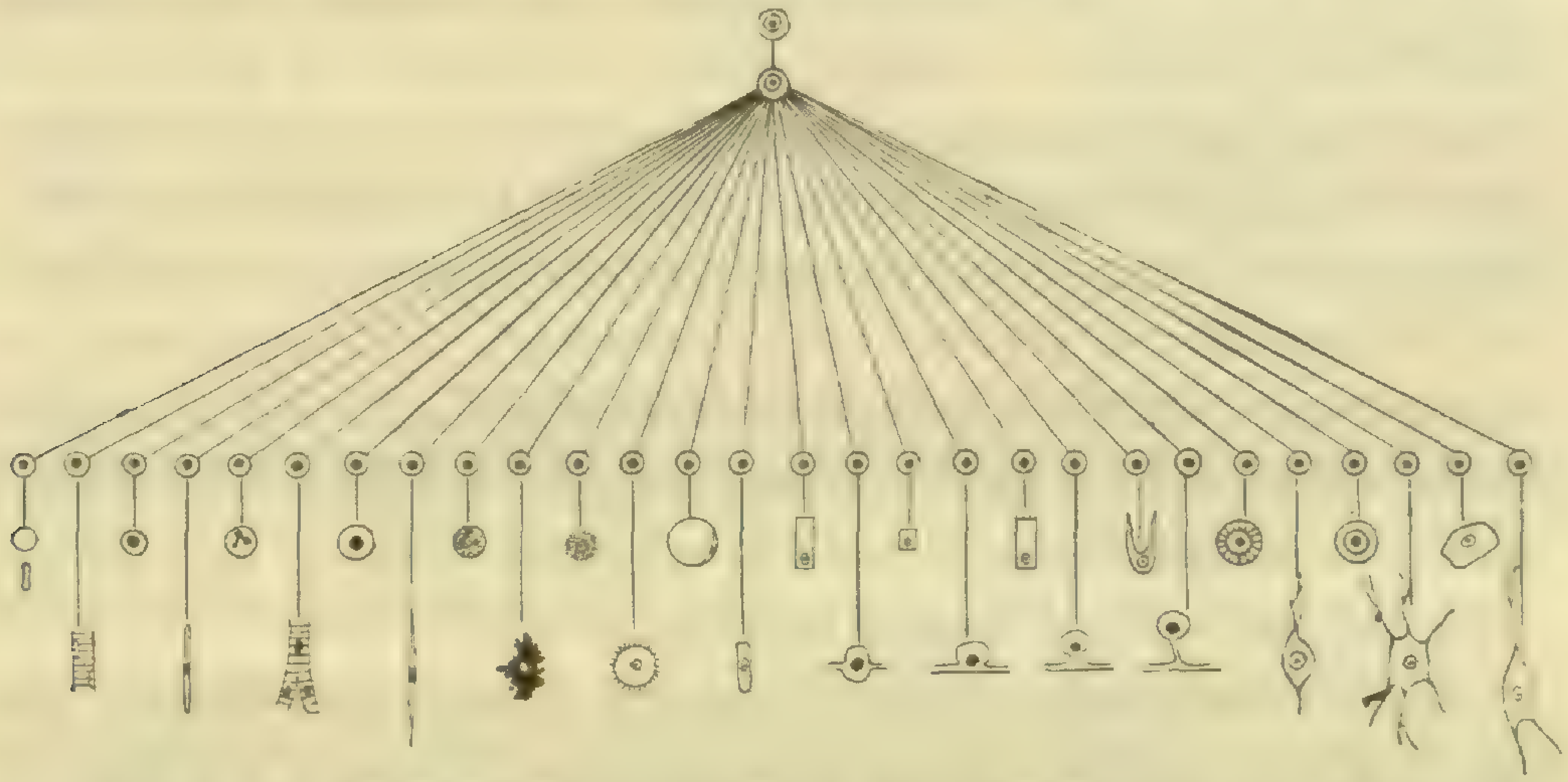

Fig. 2. In the embryonic evolution of adult tissues there are certain arbitrary stages of differentiation in which the cells may be given certain names.

During segmentation of the fertilized ovum (ovocyte) the daughter cells do not show any special morphologic characteristics of adult tissues, but are nevertheless forebearers of such tissues and may be called *protextoblasts*.

The textocytes, or tissue cells, are represented in this diagram by symbols derived from the characteristic outlines of the cells of specific tissues (Fig. 1).

After the protextoblasts align themselves into the positions of subsequent tissues they become the immediate forebearers of the tissues and may be called textoblasts. These cells develop by differentiation and specialization into the tissues (textocytes) of embryonic and adult life. Some of the cells remain undifferentiated (textoblasts) in adult life to form the reserve or regenerative cells for specific tissues when the latter are destroyed.

and functional differences. Out of such differentiation and specialization of cells, types of cells arise, groups of which constitute what are called tissues (adenotex, chondrotex, endotheliotex, epitheliotex, erythrotex, fibrotex, etc.) (Fig. 1). Two or more of the different tissues become grouped to form organs (tongue, esophagus, stomach, liver, kidneys, skin, etc.) which likewise are grouped to build up structural and functional systems (respiratory, alimentary, nervous, osseous, etc.), the combined qualities of which form the complete multicellular organ-

ism or being. Such orderly evolutional facts apply to the development of all animal and vegetable multicellular beings (Fig. 2).

Out of the essential living properties of a single cell other cells develop which have in them an exaggeration of some essential initial quality, each tissue representing an exaggeration of some one quality. Such evolutionary cytologic organization produces a communism of living units, the combined apparent and dominant purpose of which is to live and reproduce its kind.

A biologist, if asked the ultimate purpose of life, would shake his head and say he did not know, but asked the immediate and dominant purpose, would say the protection of life and this protection even at the expense of life, an apparent contradiction which has been recognized but not comprehended even by scientists. The evidence of this great protective purpose of living matter is too universal to be called to the attention of the least observing; it works automatically and in a large degree independently of the will of living beings.

This fundamental vital protective purpose forms the basis of the following consideration of cancer's place in general biology: It presupposes, and observation substantiates it, that all living cells have natural antagonists against which protection is necessary; and that there is a conflict in nature during which there is constant building up and tearing down of things living. The human body is no exception to this rule, as every physician and layman knows. The tearing down is called disease, and the rebuilding is called regeneration, repair and healing.

The partial destruction of a human tissue by animate or inanimate antagonists may be followed by its regeneration; the complete destruction may be followed by repair or replacement, but not by its regeneration.[1] The

[1] This statement may not seem to be true when applied to some of the lower forms of life such as the earthworm (*Allolobophora fœtida*) and the planaria, in which organizations certain tissues are regenerated after apparent complete destruction. The destruction is, however, not complete in such cases, because the normal regenerative power resides in other cells, which by the process of metaplasia build up tissues they do not form in the normal sequence of evolution.

degree of regeneration of tissues, according to the observations of biologists, is in an inverse ratio to the degree of their specialization and differentiation. One finds, therefore, this regenerative factor a variable and unequal quantity among tissues of the human body. The protective tissue cells (epitheliocytes) of the skin, for example, are readily regenerated if not completely destroyed over a large area; the cells of the retina, in all probability, are never regenerated even after partial destruction. Fibrocytic, erythrocytic, epitheliocytic and leucocytic tissues, in all probability, represent types, the special functions of which show the highest degrees of regeneration.

In many tissues of the body, coincidentally to normal communistic activity, there is constant or periodic normal destruction with constant or periodic regeneration, both of which depend on communistic functional activity and a constant or periodic destructive action of antagonistic agents. The amount of regeneration depends on the amount of destruction, which depends on the quality, quantity and duration of action of the destructive agent or agents.

Tissue destruction and regeneration were made the subject of investigation by the writer, in the protective cells of the human skin (Fig. 3) and in the secretory epithelium of the human mammary gland (Fig. 4). One finds in these organs that some unknown irritant or irritants of an apparent low degree of virulence, acting over a prolonged period of time, produce certain reactive cellular phenomena; there is first a destruction of the specialized and differentiated cells (textocytes). This destruction is associated with an hypertrophy of the so-called basal cells (cells of the stratum germinativum, or textoblasts) and a lymphocytic infiltration in the supporting stroma.

Space does not permit a consideration of the factor of lymphocytic infiltration. The hypertrophy of the so-called basal cells, however, is of great importance from the standpoint of the subject under consideration.

One sees clearly that nature, in building up the special-

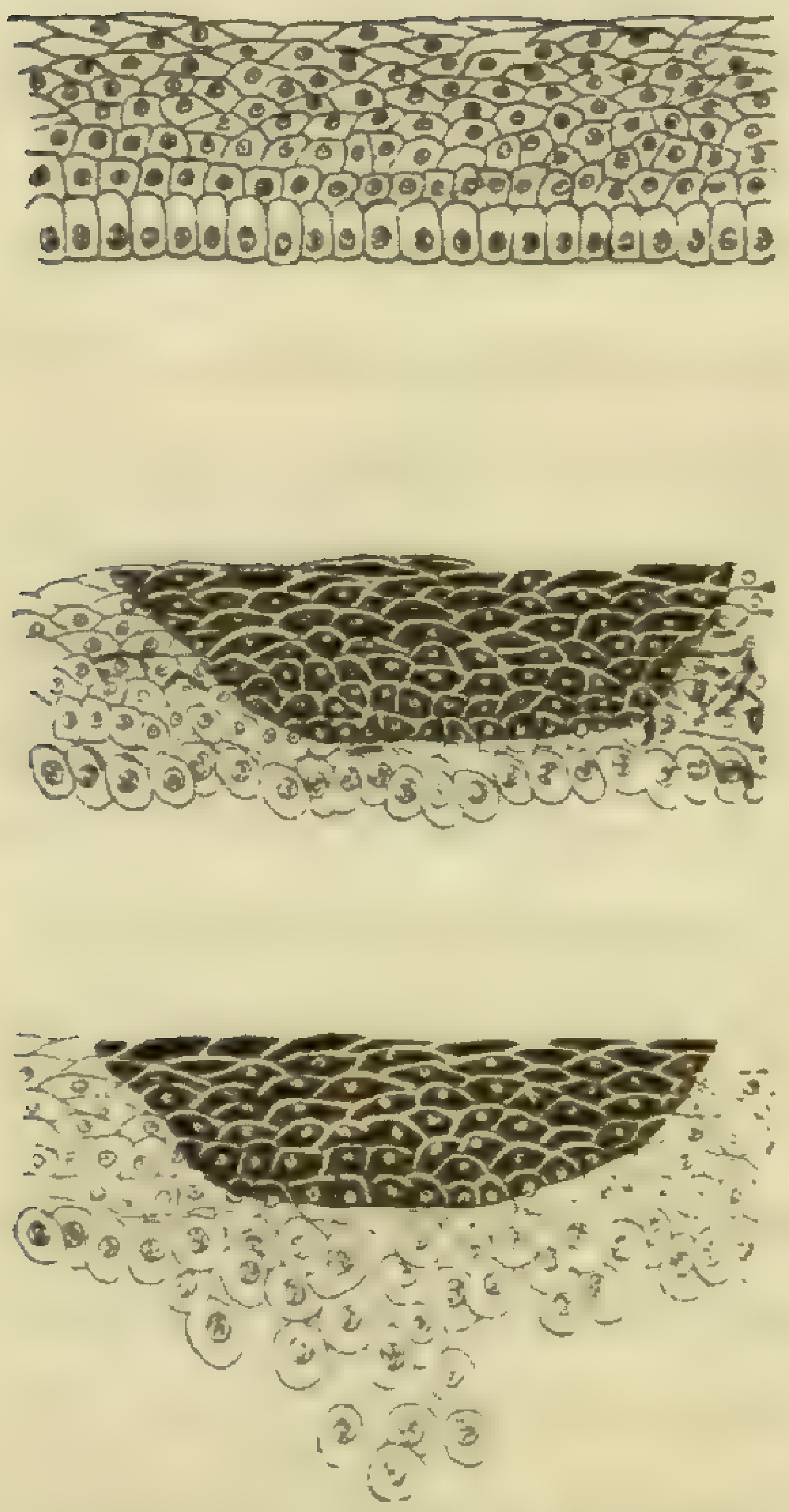

FIG. 3. Three diagrammatic histologic stages of reaction of textoblasts of the epithelium of the skin under normal and certain destructive conditions. (*a*) Normal epithelium showing the relative position of textocytes and textoblasts. (*b*) Destruction of the textocytes is indicated by the shaded portion. The response to chronic destruction is an hypertrophy or an hyperplasia of the textoblasts. This hyperplasia takes place with and without differentiation into textocytes, depending on the degree and chronicity of the destruction. In this condition it is impossible to state from the morphologic appearance whether the cells will become differentiated or remain undifferentiated. (*c*) Represents the stage of migration of the hyperplastic undifferentiated textoblasts.

ized and differentiated protective cells of the skin and the secretory cells of the mammary gland, has also made provision for an anticipated destruction, an anticipation which is no more remarkable in nature than that of the butterfly which deposits its eggs in a safe place and dies with the inherent assuredness that the eggs will some day develop into caterpillars and eventually into butterflies to continue the existence of the kind. In the case of the cells of the skin and the mammary gland, if the irritant is removed, complete regeneration of differentiated or specialized cells takes place, provided the basal cells themselves have not been completely destroyed.

Continuance of the action of the destructive agent or agents produces hypertrophy, hyperplasia and migration of the basal or regenerative cells (Figs 3 and 4). Coincidentally with such a hyperplasia the basal cells (textoblasts) do not always become differentiated to the form of the specialized squamous or secretory cells according to their communistic normal foreordination; they retain their oval or spheroidal form, become larger and produce a massed overgrowth of undifferentiated cells (Figs. 3 and 4). The degree of hyperplasia and migration varies under different and perhaps the same irritative circumstances, depending on inherited variable

factors in the basal cells the neighboring tissue cells, their food supply, natural drainage, and perhaps some unknown factors. The significant biologic facts rest

FIG. 4. Diagrammatic relation of the glandular units to the other tissues.

in the attempted cellular regeneration by hypertrophy and hyperplasia and the effort to change environment by migration, all of which may be seen not only in the breast and skin, but also in the specific cells of the hair follicle. prostatic gland and stomach (Figs. 5, 6 and 7).

A change of environment through overgrowth or migration often stimulates or allows an attempt at differentiation into the specific tissue-cells for which the original reserve or regenerative cells (textoblasts) were apparently foreordained in the normal evolution of tissues. This is evident in cancerous new growths which have migrated into other tissues, and in regional lymphatic glands, which are the favorite locations of environmental change for such migrants.

Cellular regenerative reaction takes place in one or both of two ways; there is hyperplasia with or without

differentiation. An hyperplasia with differentiation into specific tissue-cells may be called texto-typic in contradistinction to that without differentiation, which may be

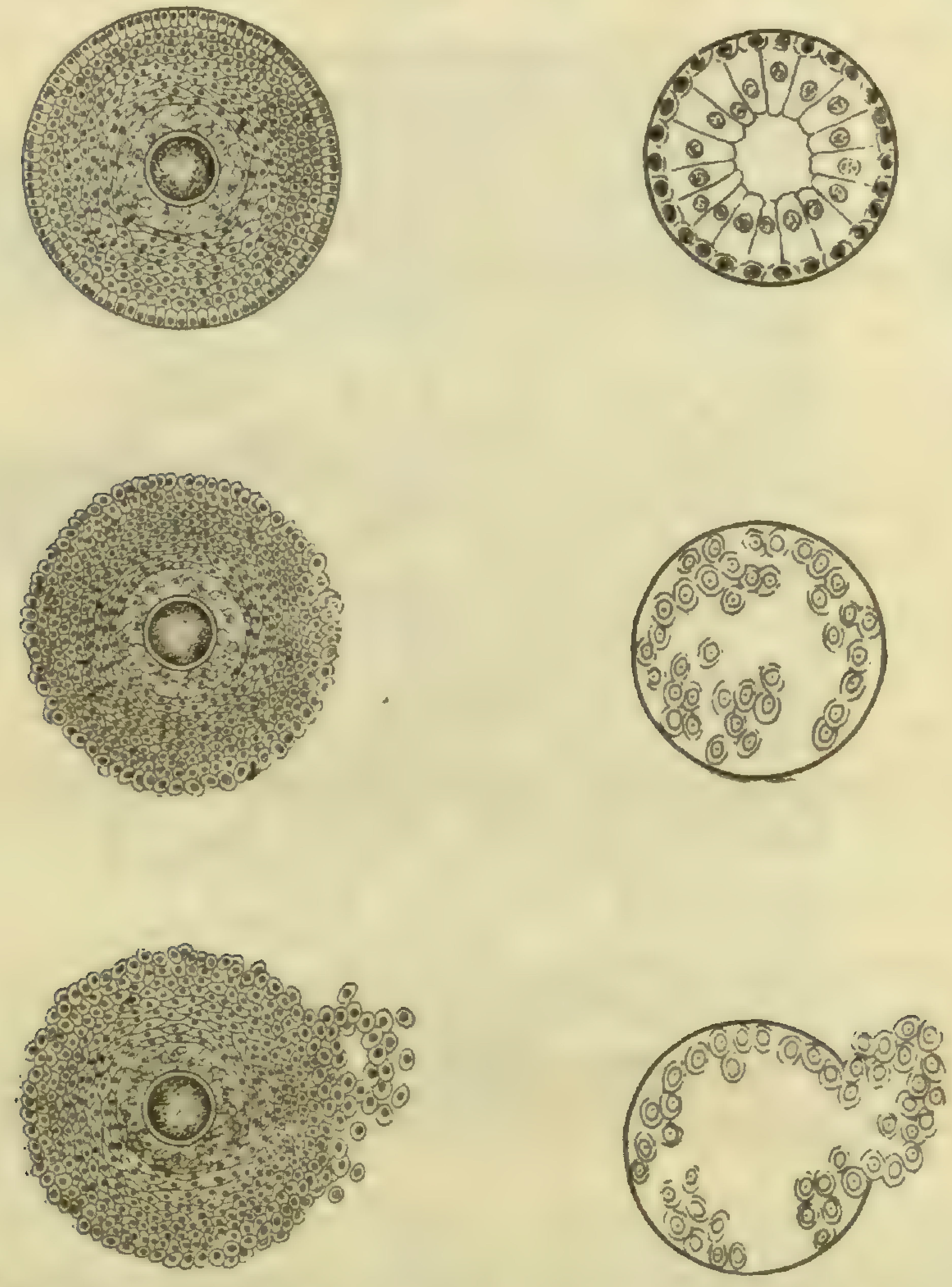

FIG. 5. The reaction to destruction of textocytes in the hair follicle. *A.* Primary pilo-cytoplasia. *B.* Secondary pilo-cytoplasia. *C.* Tertiary pilo-cytoplasia.

FIG. 6. The reaction to destruction of textocytes in the prostatic acinus. *A.* Primary adeno-cytoplasia. *B.* Secondary adeno-cytoplasia. *C.* Tertiary adeno-cytoplasia.

termed cytotypic. This occurs before and after migration.

According to writers on the subject of cancer the principal criterion for the denotation of a condition by this term consists of the destructive migration of tissue-cells. Such neoplasms have been often considered to be direct derivatives of tissue-cells, because their cells sometimes resemble those of specific tissues of organs from which they have arisen. As a matter of fact the malignant neoplastic cells (neocytes) do sometimes resemble the

FIG. 7. The reaction to destruction of textocytes in the gastric tubules. *A.* Primary adeno-cytoplasia. *B.* Secondary adeno-cytoplasia. *C.* Tertiary adeno-cytoplasia.

specific tissue-cells of the site of origin, but this is not evidence that the tissue cells themselves have been converted into the cells, which at best never are morphologically and functionally identical with the original tissue-cells.

According to the observations of the writer, the cells which constitute cancer are the progeny of the partially differentiated or reserve cells (textoblasts) which have for their natural communistic function the protective restoration of the specific tissues when the latter have been destroyed. It may be asked, how can a condition which will certainly destroy the whole organism be the result of a protective principle? This perfectly natural question can only be answered by stating a general principle in biology, namely, that regenerative changes do not always consider the communistic adaptation of the whole organism. It is a manifestation of a principle which is inherent in cells, cytologic life being primary, and tissue or organic life secondary. Thus, the planarian in response to certain stimuli produces a new head when it already possesses one; the actinian produces a new mouth on the side of its body under certain regenerative conditions. Protective migration of animals as a result of food famine leads to their complete destruction not infrequently.

In the case of the human being there is no more fitting example of a fatal, protective communistic action of cells than that which occurs when a human being obtains a severe and destructive burn about the mouth or in the esophagus. Under such circumstances the fibroblasts in the region become hypertrophic, hyperplastic, differentiated and specialized into dense, contracting scar-tissue, which, if the destruction has been great enough, may, as a communistic, regenerative, protective process, inherent in the fibroblasts, completely close the orifice of the mouth or esophagus, the result of which is starvation and destruction of the whole organism. The fibroblast's evolutionary duty in the communism is that of replacing losses of other tissues, and the duty is performed in this incidence at the expense of its own life and the life of the organism. Thus, it may be seen that communistic life is secondary to the life of the cells even in such a wonderful and complex organization as the human body.

The hyperplasia or neoplasia does not even have to be migratory from a cellular standpoint to destroy the whole organism and thereby be clinically malignant; a term which has been utilized by the medical profession largely to differentiate cancer from other neoplastic conditions which are generally conceived of as benign. Thus, a fibroid tumor of the uterus may be clinically malignant and still not show cytologic signs of the malignancy so characteristic of cancer.

Biologically speaking, protection may be divided into types—cytotypic, textotypic, organotypic, systemotypic, organismotypic, familiotypic, raciotypic and speciotypic, etc. Cancer represents the cytotypic protection which is of primary importance in all protection of living protoplasm.

From a biological standpoint the three reactions of regenerative cells of tissues to antagonistic influences are hypertrophy and hyperplasia with differentiation, hyperplasia without differentiation, and hyperplasia with migration, with or without partial differentiation. These three conditions have been termed cytoplasias (condi-

tions of cells) and have been numerically classified by the writer as primary (restauro-), secondary (expando-), and tertiary (migro-) cytoplasia. This classification is applicable to the regenerative cells of epithelial tissue of the mammary gland, prostatic gland, skin, hair follicle, stomach, fibrous connective tissue, erythrocytic tissue (red blood corpuscles) and lymphocytic tissue. These represent eight tissues out of possible nineteen or more known specific tissues in the human body. Doubtless there are other specific tissues in the human economy and perhaps some of those already mentioned may be eventually divided into other specific tissues. In all of the following tissues, adenotex, cardiomyotex, chondrotex, endotheliotex, epitheliotex, erythrotex, fibrotex, leucotex, leiomyotex, lipotex, lymphotex,, melanotex, myxotex, neurotex, osteotex, pilotex, rhabdomyotex and tendotex, with the exception of the neurotex and perhaps the myxotex, the fact has been demonstrated that all are regenerated after loss, the degree of regeneration varying considerably in the human body.

The following classification of the three biologic reactive phenomena which take place in the regenerative cells of tissues may be made:

Primary (restauro-) Secondary (expando-) Tertiary (migro-)	adeno- cardiomyo- chondro- endothelio- epithelio- erythro- fibro- leuco- leimyo- leiomyo- lympho- melano- myxo- neuro- osteo- pilo- rhabdomyo- tendo- etc..	cytoplasia.

Such a nomenclature of known reactive facts has served the writer as a convenient, simple and practical, biologic, histologic and clinical terminology. The writer does not mean that these terms should be utilized to designate neoplasms. They apply only to the tissue-reaction, which is, after all, the essential thing to be considered. Animal and vegetable neoplasms represent only phases of such reaction.

From a clinical standpoint, a hypertrophy and hyperplasia with complete tissue differentiation (restaurocytoplasia) represents tissue regeneration, which is a benign condition, since it is normally reconstructive from a communistic standpoint instead of destructive. A hyperplasia without tissue differentiation (expandocytoplasia) represents a condition of the cells in which no one can foretell whether the cells will become differentiated into tissues, and thereby be constructive, or migrate and become destructive.

Such a condition is, therefore, in the presence of science, a questionable condition. Its benignancy or malignancy, in so far as the organization is concerned, with our present knowledge, can not be forecast. The probability of possible migration may be suspected from the frequent morphologic identity of these undifferentiated cells to the migratory cells of a known malignant or cancerous condition, the only difference being their location.

Biologically considered, primary cytoplasia represents a tissue regenerative condition, the secondary cytoplasia represents a neoplastic condition, and tertiary cytoplasia represents a neoplastic migration to regions foreign to the cells in question. The whole field of tissue replacement, tissue regeneration and benign and malignant (cancerous) neoplasmata (new growths) is comprehended in these three groups.

The following diagram represents the relation of malignant (cancerous) and so-called benign neoplasms to the evolution and organization of the human body:

Fertilization (Ovocyte and spermatocyte).

Segmentation (Protexto-blasts).

Pro-differentiation[2] (Texto-blasts).

Differentiation (textocytes). — Neoplasia (undifferentiation neocytes) (Benign? or malignant?).

Differentiation (textocytes) (Benign neoplasms). — (Migration). (Malignant neoplasms).

Incomplete differentiation (Less malignant) (Pseudo-textocytes). — Undifferentiation (neocytes) (More malignant).

Briefly, in conclusion, the writer makes the following generalizations from his experience in his studies of cancer's place in general biology:

1. All multicellular organisms represent communisms of cells which have divided their labors and become specialized and differentiated to form tissues.

2. Nature has provided for the regeneration of most, if not all, tissues when the tissues are partially destroyed by antagonistic forces.

3. In many animal and vegetable tissues the regenerative cells respond to tissue-destruction in three degrees, *i. e.*, hypertrophy, hyperplasia and migration.

4. During hyperplasia with or without migration the cells sometimes attempt to differentiate.

5. Limited hyperplasia with complete differentiation produces tissue replacement. Unlimited hyperplasia without complete differentiation produces the so-called malignant neoplasms.

6. Cancer represents an unlimited hyperplasia of regenerative cells of tissues plus migration without complete differentiation.

7. Regeneration (hyperplasia) without differentiation is a cytotypic protective process.

8. Regeneration (hyperplasia) with differentiation is a textotypic protective process.

9. Cancer is a cytotypic instead of a textotypic protective process.

10. In nature cytotypic protective processes are sometimes fatal to the communism of which the reactive cells are a part.

11. All of the reactions may be designated by a simple biologic terminology which standardizes clinical, histologic and biologic facts.

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A SURVEY OF THE HAWAIIAN CORAL REEFS

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During a residence of nearly ten years in the Hawaiian Archipelago the writer has had opportunity of visiting and exploring many of the coral reefs, and has been much interested in their formation, flora, and fauna. The present paper aims to present the salient and significant facts relating to the natural history of these remarkable reefs, in compact and largely non-technical form. There is a large scattered literature (inaccessible to the average reader), dealing with the coral reefs and their life, but the writer believes this to be the first time that the following data have appeared within the confines of a single paper.

The Hawaiian Archipelago is situated in the midst of the North Pacific Ocean. It lies between latitudes 18° 54′ and 22° 14′ and 154° 48′ and 160° 13′ West Longitude, being about 2,020 miles southwest of San Francisco. Its east and west extension is nearly two thousand miles. the islands are but the apices of a titanic mountain range that rises to heights of from three to five miles from the floor of the ocean.

This long archipelago, comprising about twenty-two islands, is remarkable for the simplicity of its geologic formations. Only two classes of rock material are known in the entire group—lava and coral. There are numerous subdivisions of these groups (for example, there are many varieties of lava), but all the known rock-formations give conclusive evidence of having originated from either one of two sources—volcanic or coralline. It is extremely interesting to consider that all of these islands are compounded of two such diverse elements—one from a roaring lake of incandescent lava; the other from the age-long

labors of coral polyps. A strange "partnership," without parallel in the annals of natural history.

The islands of the Hawaiian group may be classified on this basis. The large, high islands of the eastern portion of the archipelago are composed almost wholly of lava, with small fringing reefs. The low, small islets that comprise the western extension of the archipelago are made almost wholly of coral, that is, in so far as their exposed portions are concerned. The coral formations undoubtedly rest upon a volcanic substratum. The grouping may be expressed as follows:

I. Large mountainous lava islands, forming a compact group at eastern end of archipelago; elevations over 1,000 ft.
  A. With well-developed fringing reef:
    Niihau, 1,300 ft.; Kauai, 5,250 ft.
    Oahu, 4,040 ft.
    Molokai, 4,958 ft.; Lanai, 3,400 ft.; Kahoolawe, 1,472 ft.
  B. With scanty fringing reef:
    Hawaii, 13,825 ft.; Maui, 10,032 ft.

II. Small, low islets, scattered along the western axis of the archipelago; elevations below 1,000 ft.
  C. Eroded volcanic blocks, 120–900 ft., with fringing coral reef: Nihoa, French Frigates Shoals, Gardner I.
  D. Elevated coral islands, 45–55 ft., with fringing reef: Laysan, Lisianski.
  E. Typical coral atolls: Pearl-and-Hermes, Midway, Ocean.
  D. Reefs with visible surf, but no exposed coral: Maro Reef, Dowsett's Reef.

The entire series, named in sequence from east to west, is: Hawaii, Maui, Kahoolawe, Lanai, Molokai, Oahu, Kauai, Niihau, Nihoa, Necker, French Frigates Shoal, Gardner, Dowsett's Reef, Maro Reef, Laysan, Lisianski, Pearl-and-Hermes, Midway, Ocean. The two extremes—Hawaii and Ocean Island—present a contrast of wonder-

ful vividness. Mauna Loa, the greatest active volcano on the planet, dominates the island of Hawaii. Its colossal dome is crowned by a summit lake of reverberating liquid lava, with spectacular displays of high-jetting fire fountains. The bulk of the island is still growing, through intermittent outpourings of lava. Ocean Island, on the other hand, is the last white fragment of a subsiding coral-crowned mountain—perhaps a dead volcano, that may have resembled Loa in many respects, but which has been drawn inexorably into the abysses of the Pacific. One represents the culmination of the volcanic forces; the other the climax of coral work—an atoll on a tropic sea.

Of the larger eastward islands, Kauai and Oahu are of particular interest, as they have the largest coral reefs, and support the most luxuriant marine life. The reefs are all of the fringing or platform type, and vary in width from a few hundred feet to half a mile. Reefs are well developed along the southern or leeward shores of the two Islands mentioned, and also, to a lesser degree, along the northern coasts. Oahu is almost encircled by coral reefs, whereas Kauai, Molokai, and Maui have numerous coastal stretches wholly free from coral. The little island of Niihau, to the west of Kauai, has considerable coral reef.

It is significant to note that although the majority of corals, particularly the more massive reef-building forms, occur only in the shallow waters of tropic seas, there are a number of species that inhabit deep, cold waters. *Lophohelia prolifera* and *Dendrophyllia ramea*, for example, form dense beds at depths of from 600 to 1,200 ft. off the coasts of Norway, Scotland, and Portugal. The general requirement, however, is shallow water whose mean temperature does not fall below 68° F., and the reef-building species do not flourish unless the temperature is considerably higher. Although a single Hawaiian species of mushroom-like coral (*Bathyactes Hawaiiensis*) was dredged by the *Albatross* from a depth of nearly 7,000 ft., most of the Hawaiian forms live in waters of

6–150 ft. depth. Of the 34 Hawaiian genera, 14 habituate this shallow-water zone throughout the archipelago, and 10 of these occur on the leeward reefs of Oahu between Leahi and Pearl Harbor.

Dana's[1] comprehensive statement concerning the reef-building corals may be compactly summarized. He states that it is important to have a correct apprehension of what are those reef species as distinct from those of colder and deeper seas. The coral-reef species of corals are the following:

1. In the *Astræa* tribe, all the many known species.
2. In the *Fungia* tribe, almost all the known species.
3. In the *Oculina* tribe, all of the *Orbicellids;* part of the *Oculinids* and *Stylasterids;* some of the *Caryophyllids, Astrangids,* and *Stylophorids;* all of the *Pocilloporids.*
4. In the *Madrepora* tribe, all of the *Madreporids* and *Poritids;* many of the *Dendrophyllia* family.
5. Among *Alcyonoids,* numerous species of the *Alcyonium* and *Gorgonia* tribes and some of the *Pennatulacea.*
6. Among *Hydroids,* the *Millepores* and *Heliopores.*
7. Among Algæ, many *Nullipores* and *Corallines.*

He further states that

> Through the *torrid* region, in the central and western Pacific, that is, within 15° to 18° of the equator, where the temperature of the surface is never below 74° F. for any month of the year, all the prominent genera of reef-forming species are abundantly represented. The Hawaiian Islands . . . are outside of the torrid zone of oceanic temperature, in the *subtorrid,* and the corals are consequently less luxuriant and much fewer in species. There are no Madrepores, and but few of the *Astraea* and *Fungia* tribes; while there is a profusion of the corals of the hardier genera, *Porites* and *Pocilliporæ.*

The more abundant reef builders, at moderate depths, are the madrepores, astræids, porites and meandrines. At depths of 90–120 ft. the millepores and seriatopores predominate. The great field of coral development thus lies between low water and 120 ft.

Dana's classification of reef-formations is useful in surveying the Hawaiian reefs:

[1] James D. Dana, "Corals and Coral Islands," 1872.

1. *Outer reefs,* or reefs formed from the growth of corals exposed to the open seas. Of this character are all proper barrier reefs, and such fringing reefs as are unprotected by a barrier. All of the larger Hawaiian reefs are of this character.

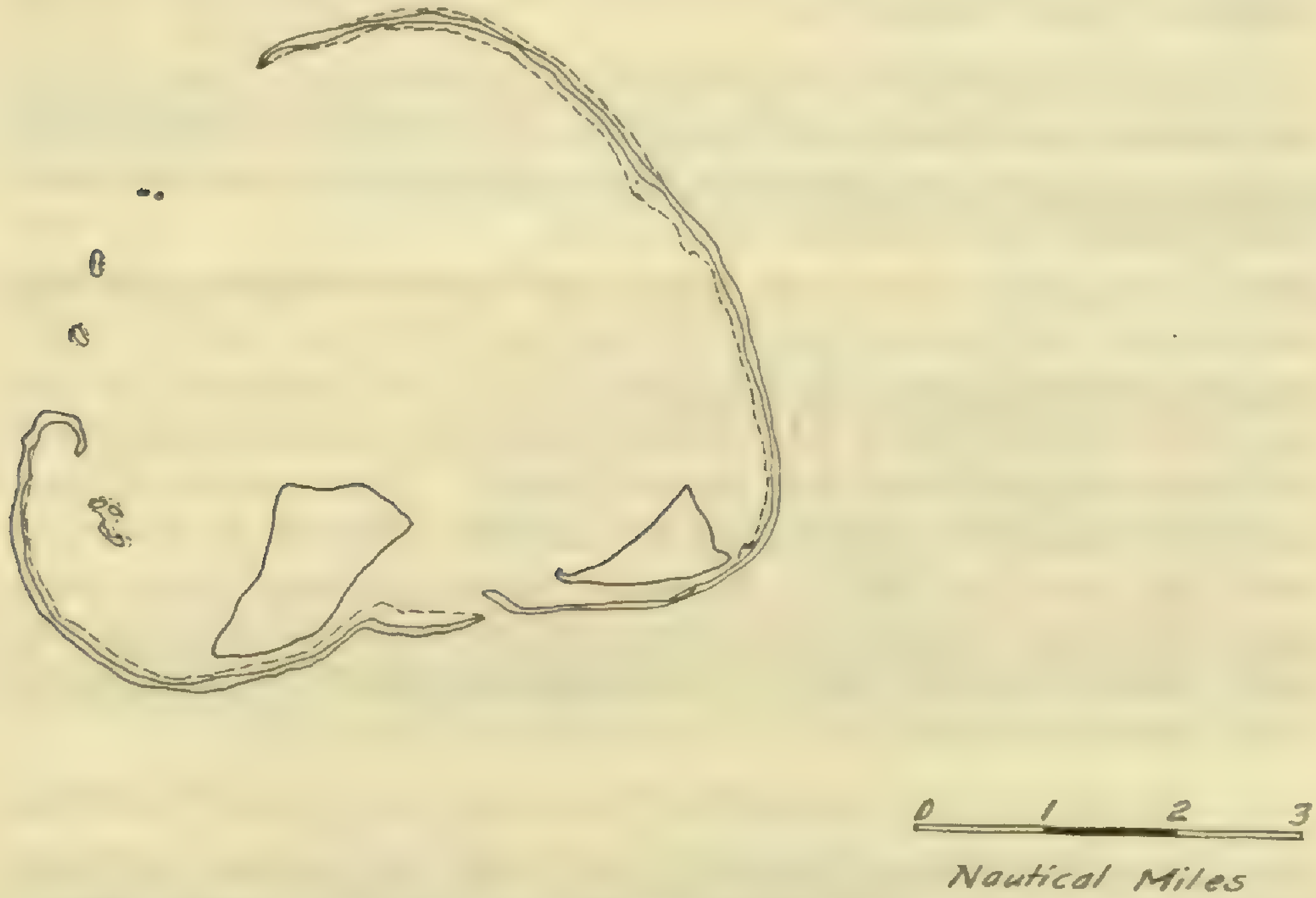

FIG. 1. Midway Island. A nearly complete circular coral atoll, about 16 miles in circumference; area of lagoon about 38 sq. miles; several low sand islets in the lagoon.

2. *Inner reefs,* or reefs formed in quiet waters between a barrier and the shores of an island. The reefs of this type are very rare in Hawaii; usually they are mere hummocks in the lagoon of the fringing reef.

Kaneohe Bay and Pearl Harbor, on Oahu, are essentially large drowned valley regions, converted by subsidence into land-locked bays, which have become more or less completely barred and filled by coral growths. Were there not such large quantities of fresh, mud-laden water poured into these bays, they would be veritable coral wonderlands, for it is in protected waters of inner channels or lagoons that corals attain their finest development, and the "richest views are presented to the explorer of coral scenery."

The marine flora and fauna in these bays presents

many contrasts with those of the true lagoons and outer reef rims. All of the pure-sea-water-requiring organisms are wholly absent or rare, and in their places one finds a large series of brackish water and silt-loving forms. The generalization is quite accurate for the Kaneohe and Pearl Harbor inner reefs that

> The main distinction between the inner and outer reefs consists in the less fragmentary character of the rocks in the former case, the less frequent accumulations of débris on their upper surface, and the more varied features and slopes of the margins. . . . There is to be found about inner reefs, over large areas, solid white limestone, showing internally no evidence of its coral origin, and containing rarely a shell or other imbedded fossil. It is a result of the consolidation of the fine coral sand or mud that is made and accumulated through the action of the light waves that work over the inner reefs. Other portions of reef consist of branching corals, with the intervals filled in by sand and small fragments; for even in the stiller waters fragments are to some extent produced. A rock of this kind is often used for buildings and walls on the island of Oahu. It consists mainly of *Porites,* and in many parts is still cavernous, or but imperfectly cemented.[2]

3. *Channels or seas* within barriers, which may receive detritus either from the reefs, or from the shores, or from both these sources combined. These channels correspond to the lagoons of the fringing reef, except that the channels are much larger. The Hawaiian lagoons are generally floored with coral sand, indicating that reef erosion is more rapid than coast erosion.

4. *Beaches and beach formations,* produced by coral accumulations on the shore through the action of the sea and winds. Beaches and dunes of coral sand are common on the islands of Molokai, Oahu, Kauai, Laysan, Midway, Ocean, etc.

Of the three great classes of coral reefs—fringing, barrier, and atoll—the first and last only have representation in the Hawaiian Archipelago. The fringing reefs are platforms of coral limestone which extend but a relatively short distance from the shore. The seaward edge of the platform is characteristically somewhat higher than the inner portion, and is usually awash at low tide. The reef

[2] Dana, *loc. cit.*

is cut by more or less numerous channels, which mark those places where streams flow down from the land. There is usually a lagoon—of sufficient depth to be navigable by canoes or small boats—between the reef rim and the shore. The outer wall of the fringing reef is steep, and in the Hawaiian Islands descends abruptly into deep water. The reef rim is the region of most active coral growth, the shoreward coral being gradually killed by fresh water and the deposition of mud and sand.

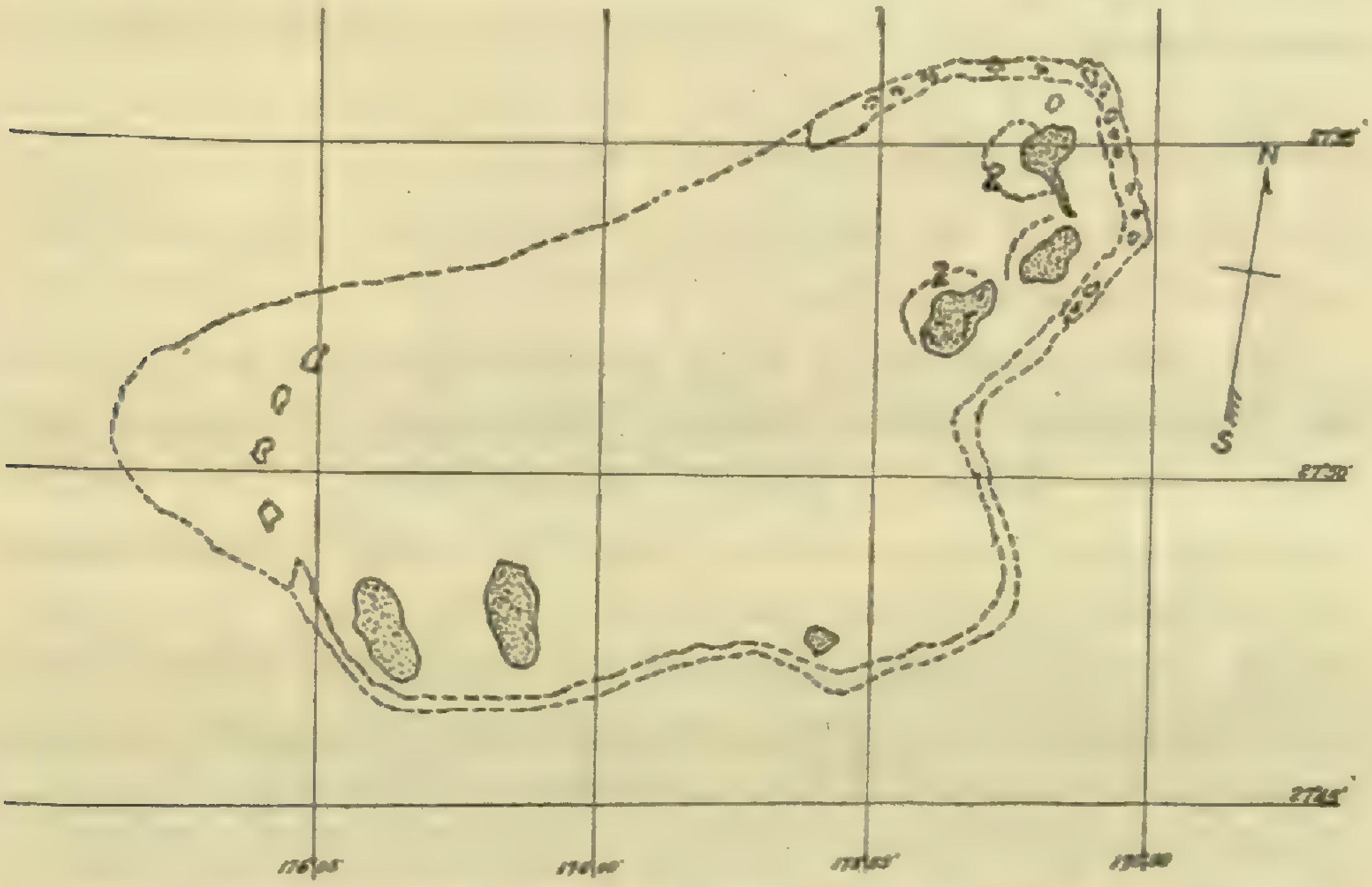

FIG. 2. Pearl and Hermes Reef. An irregular, oval coral atoll, 42 miles in circumference; area of lagoon about 80 sq. miles; numerous low sand islets in the lagoon. The soundings (2) are in fathoms.

Barrier reefs may be considered as fringing reefs upon a large scale. Although rare in the North Pacific Ocean, there are many fine examples in the South Pacific. The grandest in the world is the Great Australian barrier reef, which is 1,250 miles long, and supports a wonderfully rich marine life.

An atoll is an annular or ring-shaped reef, either awash at low tide or surmounted by several islets, or less frequently by a complete circle of dry land surrounding a central lagoon. The outer wall of the atoll generally descends with a very steep but irregular slope to a depth of

3,000 ft. or more. The central lagoon is seldom more than 60 ft. deep, and is often much less. There are usually one or more navigable passages leading from the lagoon to the open sea.

The thickness of the Hawaiian reefs is an engaging subject for speculation. Many of the reefs are undoubtedly several thousand feet thick at their seaward margins. Dana writes:

> Could we raise one of these coral-bound islands from the waves, we should find that the reefs stand upon submarine slopes, like massy structures of artificial masonry; some forming a broad flat platform or shelf ranging around the land, and others encircling it like vast ramparts, perhaps a hundred miles or more in circuit.

The late Dr. S. E. Bishop, of Honolulu, estimated the depth of the coral at Barber's Point, Oahu, to be 2,500 ft.

Our first exploration of a Hawaiian coral reef, some ten years ago, made a lasting impression, so novel and vivid were those initiatory experiences. The tropic morning was fine and clear, with the clouds heaped along the mountains, and the seaward sky flawless. The trade winds were unusually quiet and the tide was at lowest ebb. All conditions were most favorable for a detailed examination of the reef. My comrade and I embarked in a native outrigger canoe and paddled from the well-known Waikiki Beach, near Honolulu, to the white surf-lines of the reef-rim. This is one of the richest portions of the Oahu fringing reef, from the biological standpoint. We were clad in bathing suits and provided with suitable collecting apparatus and water-boxes—glass-bottomed boxes by means of which the sunlit translucent waters are easily surveyed.

Arriving at a suitable location, a thousand feet from the shore, where the water was scarcely two feet deep, we anchored the canoe and prepared for wading. We were equipped with old shoes to protect our feet from the coral (which can cause very painful and slow-healing wounds); with broad-rimmed hats to protect eyes, face, and neck from the intense glare of sun and water; with hammers

for breaking up the coral blocks and for loosening material; and with sundry haversacks, wide-mouth bottles, formalin, etc. For three entrancing hours we wandered over the ledges, knolls, and sandy pockets of the reef, bewildered by the luxuriant diversity of marine life. Fantastic clumps of living coral, a large number of strange molluscan species; bright-spotted crabs and other

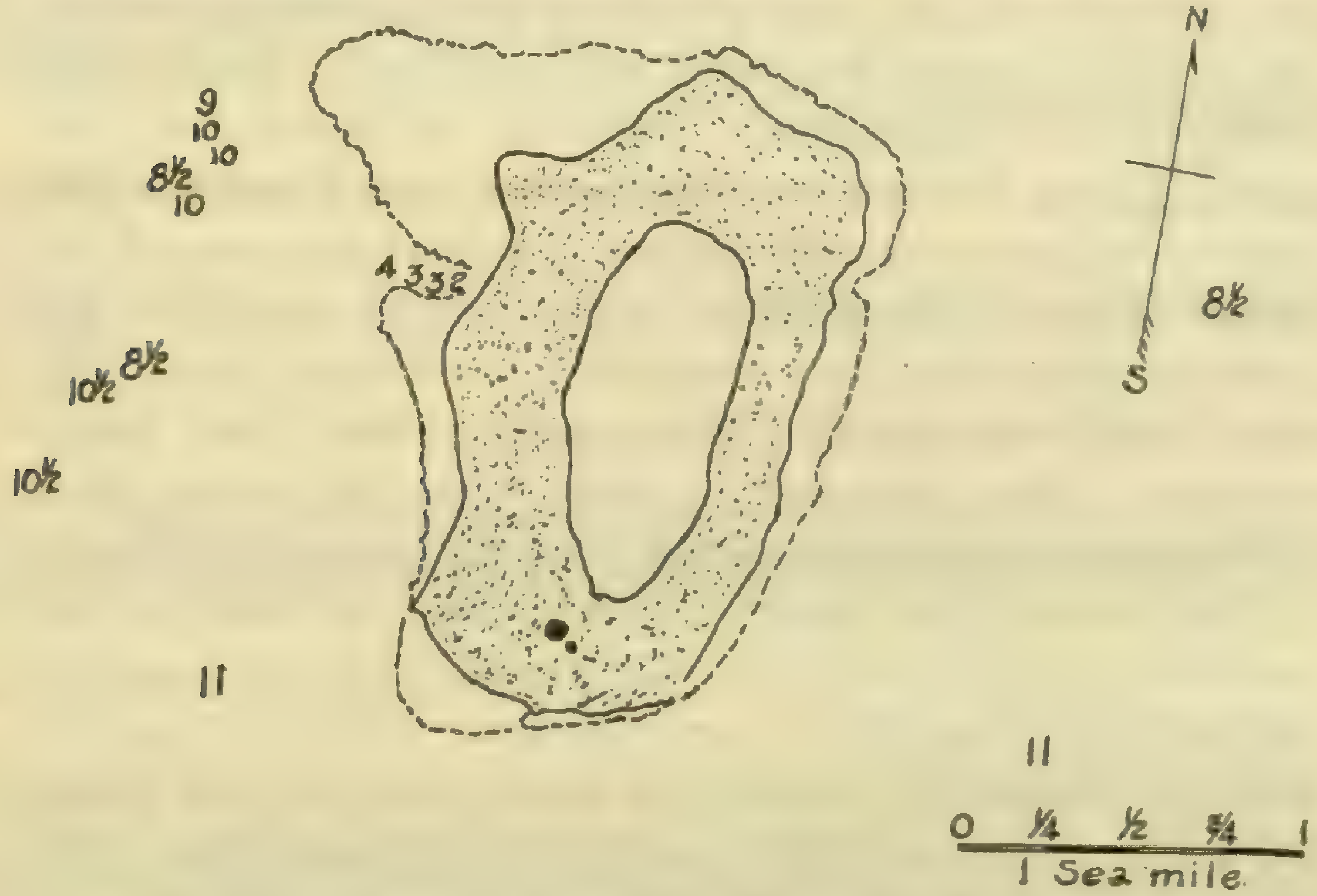

FIG. 3. Laysan Island. An elevated coral island, with a central lagoon. The soundings are in fathoms, as in all the maps. The dotted line indicates the reef rim; this also applies to all the maps.

crustaceans in an array of shapes and sizes; colonies of sea-urchins; spidery-armed brittle-stars; exquisitely beautiful hydroid colonies; bizarre-hued holothurians; and everywhere marine algæ of many tints and shapes, representing a long list of interesting genera. Gorgeously colored fishes, small and large, lurked in the shadowy reef pools, and evaded prolonged inspection. It is impossible to describe the profound impression produced by one's first sight of the strange and fascinating reef-world.

The coral fauna of the Hawaiian reefs, although not as rich nor as diversified as those of more tropical waters, is not to be regarded as scanty. Dr. T. Wayland Vaughan, who thoroughly investigated the *Albatross* and Bishop

Museum collections, reports 15 families, 34 genera, and 123 species, varieties and forms. As Bryan[3] states,

> Some idea of the richness of the coral fauna of any given locality can be gathered from the fact that the reef and shallow waters along the south side of Oahu, but especially at Waikiki, yielded examples of thirty-four of the species enumerated.

Of the Hawaiian stony corals (Madreporarians) the genus *Porites* is the most abundant and is represented by the largest number of species and varieties. *Pocillopora* ranks next in importance, followed by *Montipora, Pavonia, Favia, Leptastrea, Cyphastrea,* and *Fungia.* The last-named genus merits special mention because of the unique shape of the skeleton, which closely resembles the inverted head of a fully expanded mushroom, hence the name mushroom coral. These are solitary, and fairly common. They are usually found lying flat on the floor of little pools or pockets along the outer edge of the reef.

The corals, like many other groups of marine organisms, are remarkable for the variety and brilliancy of their color during life. Those who know only the bleached museum specimens have little conception of the living tints, some of rare delicacy, others of brilliant hue. The Hawaiian reefs, although they do not show colors as striking as those of the South Pacific and Indian Oceans, are not lacking in color, and the "Coral Gardens" are becoming far-famed as tourist attractions. Pink, yellow, green, brown, purple and scarlet are represented in many shades and combinations.

One of the most beautiful of the Hawaiian corals is a highly precinctive species, *Dendrophillia Manni,* which is known only from Kaneohe Bay, on the island of Oahu. The living coral is a rich deep orange red. There are numerous short branches, each of which is surmounted by a single bright orange polyp. When fully expanded the polyp is about three quarters of an inch long, and resembles a miniature sea-anemone. The polyp can withdraw completely within its cup. This species is rare,

[3] William Alanson Bryan, "The Natural History of Hawaii," Honolulu, 1915.

occurring only here and there along the margins of the little coral islands in Kaneohe Bay.

Fig. 4. Lisiansky Island. A low, oval island of coral sand, two miles by three miles; the lagoon empty of water. The surrounding reef extends six or seven miles from the isle.

The famous black coral, *Antipathes abies*, is absent from the Hawaiian reefs, although it has a wide distribution in the Indian and South Pacific Ocean. It grows to considerable size in the tropical waters of the Great Barrier Reef of Australia.

The eight-rayed corals (*Alcyonaria*) are very rare on the reefs, but occur in fair abundance in the deep offshore waters. The *Albatross* collected about 70 new species, 40 of which were new to science. The Red or Precious Coral of commerce, *Corallium rubrum,* does not occur in the Hawaiian Archipelago. It is most abundant in the Mediterranean Sea, although also occurring off the coasts of Ireland and Africa. Related species of slight commercial value have been obtained off Mauritius and near Japan.

The *Alcyonacea,* organ-pipe and blue corals, are represented in Hawaii by only five species; the *Gorgonacea,* sea-fans, by 16 species; and the *Pennatulacea,* sea-pens, by 48 species. Many of the Hawaiian members of these groups are of great beauty, but are never found *in situ* on the reefs, and when rarely washed ashore are badly mutilated by the waves. Some of the species are phosphorescent.

The typical Hawaiian fringing reef exhibits five distinctive biological zones. This zonation parallels the shore-line, and is best developed on those reefs which possess wide lagoons and a well-defined outer margin or rim.

1. *Beach or Inshore Waters.*—The shallow inshore waters, varying in depth from 6 to 36 inches, sustain a number of the quiet-water algæ, such as *Enteromorpha* spp., *Hypnea nidifica, Gracilaria, Chætomorpha, Ulva, Chondria, Liagora,* etc. The bottom is of coral sand or mud, more or less contaminated by volcanic soil washed from the lowlands. The water is often mingled with relatively high percentages of fresh water. The nature of the bottom depends largely upon the proximity of fresh-water streams and of the reef-rim. In many places where the surf is heavy and reef material abundant, the bottom is pure white coral sand, with practically no rock or mud. In other districts there are large mud-flats exposed at low tide; the limestone pavement is covered with a thin sheet of mud, with little sand. Every gradation may be found between these two extremes. At the mouths of streams and at numerous other places along the coasts where fresh-water springs exist below tide-level, the inshore water is so fresh as to prohibit the development of the strictly marine species.

2. *Partially Submerged Rocks.*—In some places the beach and shallow waters are devoid of rock masses, but in general one finds partially submerged rocks scattered all along the coasts. These may be either close inshore, in the form of ledges or detached fragments, or may lie

at varying distances from the shore. In any case they distinctly indicate, by their horizontal banding of algal and hydroid life, the ranges of high and low tide. The rocks are either of consolidated reef coral or of black basaltic lava; tufa rocks, and sedimentary coral sandstone are infrequent. Some groups of marine organisms show strong preference for the coral rock, others for the lava rock. The rocks may be in somewhat protected situation or may be exposed to the full force of the surf. The following genera contain algæ which are representative of the kinds that withstand the constant battering of the waves: *Gymnogongrus, Codium, Haliseris, Asparagopsis, Dictyota, Gelidium, Ahnfeldtia, Porphyra.* The controlling factor in the alga-flora of the partially submerged rocks seems to be the circulation of pure, well-oxygenated sea water. Rocks in stagnant or impure water support a scanty flora as compared with those of the surf-swept localities.

3. *Pools.*—Beyond the rock litter, although sometimes interspersed by it, lies the zone characterized by numerous pools or pockets. These cup-like depressions in the lagoon floor vary in size from little pockets two or three feet in depth and diameter to large pools twenty or thirty feet in depth and diameter. In wading or paddling over the reef, the pools are easily distinguished by the darker tint of their waters as contrasted with that of the shallow lagoon. These pools in the floor of the lagoon are not to be confused with the tidal pools, that lie along the beaches, and are entirely detached at low tide. The lagoon pools are inhabited by a great variety of algæ and animals that prefer these shadowy havens to the exposure of the shallows or the outer reef. The bottom of the pool may be covered with clear coral sand, or coral débris, or masses of living coral; its alga-flora will depend upon its depth and the resultant intensity of illumination.

The following are typical alga genera that have representatives in the lagoon pools: *Corallina, Peysonnelia, Grateloupia, Ceramium, Amansia, Polysiphonia, Chon-*

dria, Laurencia, Martensia, Champia, Wrangelia, Galaxaura, Padina, Sphacelaria, Hydroclathrus, etc.

4. *The Lagoon.*—The entire region between the beach line or strand and the seaward rim of the reef is properly designated as the lagoon, but for the purposes of this description the term will be restricted to the deeper waters, which are usually located about midway between the beach and the reef-rim. As one approaches the lagoon wading becomes impossible, the water deepens to eight, twelve or twenty feet, but again becomes shallow as the outer edge

Fig. 5. French Frigates Shoal. Crescentic atoll, with numerous low sand islands, and several high rocky volcanic isles; area of shoal about 30 sq. miles. The reefs are extensive.

of the reef is reached. The water of the lagoon is placid, clear, and in normal weather very translucent, so that the bottom receives good illumination. Although a number of the smaller algæ grow upon the floor of the lagoon, the region is comparatively barren as compared with the shallower waters on either side. The lagoon floor is a region of coralline and animal life, rather than of plant life. The quantities of sand and silt that are constantly washed over the floor from the disintegrating reef-rim render it difficult for plants to maintain themselves. The floor is so irregular in topography that collecting is very difficult;

dredging is almost impossible, and diving is both laborious and unsatisfactory.

5. *Reef-Rim.*—Upon paddling across the lagoon to the outer rim of the reef, one comes to shallow water, where the heavy combers break and where wading is again possible. This zone is a favorite fishing-ground of the native Hawaiians, as it abounds with plant and animal life. The highest portions of the rim are usually exposed at low tide; at high tide they are covered by 18–24 inches of water. There are many table-rocks or shoals, with deep channelways between. The rim is not regular or symmetrical; there are many indentations, crags, débris slopes, pools, hummocks and sandy spots. Almost all of the visible coral of this region is living coral, associated with an abundance of corallines, bryozoans, hydroids and red and brown algæ. Some of the algal genera that are confined largely to the outer reef-rim are: *Codium, Asparagopsis, Gymnogongrus, Porphyra, Turbinaria, Dictyota, Haliseris, Gelidium*, etc. Many of the species that inhabit these turbulent and surf-churned waters are not the tough, cartilaginous forms, but are very delicate and fragile species, that apparently survive the wave action because of their very delicacy. This is particularly true of some of the finer red algæ.[4]

Highly important on the Hawaiian reefs are the coralline or stony algæ or nullipores. A number of genera—

[4] Some of the representative marine algæ of Hawaii that are common on the coral reefs and shallows are: *Oscillatoria bonnemaisonii, Phormidium crosbyanum, Lyngbya semiplena, L. majuscula, Hydrocoleus cantharidosmus, Nodularia Hawaiiensis, Hormothamnion solutum, Scytonema fuliginosum, Calothrix æruginea, Ulva* spp., *Enteromorpha* spp., *Chætomorpha pacifica, Cladaphora* spp., *Bryopsis plumosa, Caulerpa taxifolia, Halimeda* spp., *Codium* spp., *Valonia* spp., *Dictyosphæria favulosa, Microdictyon umbilicatum, Ectocarpus* spp., *Sphacelaria* spp., *Hydroclathrus cancellatus, Asperococcus bulbosus, Turbinaria ornata, Sargassum* spp., *Padina pavonia, Dictyota* spp., *Liagora decussata, Galaxaura lapidescens, Scinaia furcellata, Gelidium* spp., *Wrangelia penicillata, Gymnogongrus* spp., *Ahnfeltia concinna, Gracilaria* spp., *Hypnea nidifica, H. armata, Plocamium sandvicense, Martensia flabelliformis, Asparagopsis sanfordiana, Laurencia* spp., *Chondria tenuissima, Polysiphonia* spp., *Amansia glomerata, Ceramium* spp., *Grateloupia filicina, Peyssonnelia rubra, Corallina* spp., *Lithothamnion* spp.

Lithothamnion, Corallina, Mastophora, and others—are abundant on the reefs, and undoubtedly have been active as reef-builders. The importance of the lime-secreting algæ was overlooked by the earlier students of coral reefs, but is now receiving adequate consideration. Howe[5] shows that these forms work effectively at greater depths and at lower temperatures than do the true corals, and that they are much more generally and widely distributed than the latter.

The Hawaiian coralline algæ inhabit the shallow waters, as well as occurring at considerable depths. In the former situations they form beautiful rose, purple and lavender incrustations. On the faces of cliffs that are washed by the sea these incrustations appear as conspicuous bands, extending from high-tide mark or the uppermost wash of the surf down to the zone of minimum illumination. The lower margin of the coralline zone has not been investigated in the Hawaiian Islands, but in other island groups they flourish at 1,000 ft. depth. In the coralline zone are also many of the calcareous hydrozoa.

Sponges of many species, sizes and colors abound in all protected portions of the reefs, but have never been made the subject of critical taxonomic study. They range from tiny, fragile forms, the size of a shoe-button, up to coarse horny masses as large as a man's head. The lesser species are common on the coral-rock litter in the lagoons. The larger forms inhabit the deeper waters, and are torn from their anchorage only by the occasional severe storms. After a period of southerly storms, for example, the leeward beaches are littered with these large, tough sponges, which average eight inches in diameter.

The range of color is bizarre and striking. In a single afternoon's collecting one may pick up, in the shallow water, species of bright red, pale yellow, rich purple, dull brown, creamy white, green, and dead black pigmentation. Dredging reveals others which add to the chromatic series. Most of the sponges are of the encrusting type, the body

[5] M. A. Howe, "Building of Coral Reefs," *Science*, 36: 837–842, 1912.

conforming to the substratum and having no definite shape. The *Calcarea* are not uncommon in the littoral region, especially in sheltered situations among rocks and seaweed. These and the true horny sponges (*Ceratosa*) have not been found below 2,700 ft. The sponges found at the greatest oceanic depths are members of the *Hexactinellida* and *Choristida* of the *Non-Calcarea.*

FIG. 6. Island of Oahu. Showing extensive development of coral reefs ⟍⟍ and elevated coral limestone ///. Note the abundance of coral in the vicinity of Pearl Harbor (the fan-shaped bay on the south coast), Kane-ohe Bay (on the northeast coast) and along the southern shores.

The Hawaiian sponges have few or no natural enemies, and do not appear to be edible to fishes, crustaceans or molluscs. Innumerable lowly forms, however, inhabit their tissues, for shelter, if not for food. The interior of any one of our common reef sponges is almost sure to be found teeming with minute crustaceans, annelids, molluscs and other invertebrates.

None of the Hawaiian species have been utilized commercially and no serious attempts have been made to in-

troduce and establish the valuable species from other parts of the world. All of the commercial sponges belong to the two genera *Euspongia* and *Hippospongia*, which do not occur on the Hawaiian reefs. Such an enterprise, if undertaken with thorough scientific supervision, would unquestionably meet with success. There are many areas along our reefs where the sponges could be established. With adequate labor and marketing arrangements a steady development of the industry would be assured.

It is of interest to note that of the fresh-water sponges, *Spongillinæ*, a group which is widely distributed in all parts of the world, no representatives have been taken in the Hawaiian Islands.

Jellyfish are of casual occurrence along our reefs. The smaller forms are chiefly Hydrozoan medusæ; the larger ones are Scyphozoans. A relatively few species are known and the life-cycles of these are not known in detail. A number of the tiny species are phosphorescent, and on clear nights when the sea is calm and other conditions are favorable, they give beautiful luminous effects. In paddling along the reef in an outrigger canoe, on such a night, the paddles, at every stroke, drip with tiny stars. Many of the larger species have gonads, tentacles, radial canals, or other organs brilliantly pigmented.

The large forms attain diameters of 8–12 in. and sometimes appear in great numbers in quiet, protected waters. Pearl Harbor, for example, which is almost wholly landlocked, is a favorite habitat. At low tide, in other parts of the islands, along the coral beaches one sometimes finds great numbers of jellyfish stranded and slowly deliquescing.

In addition to the true jellyfish the reefs support a rich hydrozoan or marine hydroid fauna. The littoral species have not been studied taxonomically; the *Albatross* collections were made at depths of 60–3,000 ft. These latter comprised 49 species, representing 27 genera and 11 families. The shallow-water zoophytes or hydroids are abun-

dant in all protected situations; many forms also inhabit the surf-beaten rim. *Sertularia, Plumularia* and *Campanularia* are well-known genera. The species are all of small size and superficially resemble in habit, color and habitat the more delicate marine algæ.

The false corallines or *Hydrocorallinæ* are also very abundant and have played an important rôle, as have the coralline algæ, in the construction of the Hawaiian reefs. These colonial animals resemble delicately branching corals; their bleached and rather fragile skeletons are common on the beaches. When alive the corallines are of various tints of pink, orange and salmon, and add bright touches of color to the brilliant ensemble of the reef. The *Hydrocorallinæ* occur only in tropical seas; *Millepora* and *Stylaster* are typical genera.

That remarkable order of free-floating colonial hydroids, the *Siphonophora,* is well represented in all tropical waters, and has numerous forms in the Hawaiian marine fauna. This group exhibits the greatest diversity of form. The common "Portugese man-of-war," *Physalia utriculua,* with its brilliant peacock-blue float and long retractile tentacles, is abundant along the reefs and shallows, and like the jellyfish, is often cast ashore in enormous numbers. The tentacles contain powerful batteries of stinging capsules; the wounds are intensely painful, and so this lovely evanescent creature is dreaded by bathers. Other well-known genera are *Halistemma, Diphyes, Porpita* and *Vellelo. Porpita pacifica,* the sea-money, is a beautiful blue-fringed disc about 1½ in. in diameter. *Vellela pacifica* is also abundant at certain seasons. It resembles *Physalia,* but has much shorter tentacles.

Sea-anemones, *Actiniaria,* are abundant along the Hawaiian reefs, but no taxonomic studies have been made. A number of species inhabit the inshore pools whose waters are periodically renewed by waves or tides; others may be found on the floor of the lagoon, and still others on the protected sides of rocks which stand in the heavy

surf. The colors most frequently observed are shades of tan, olive and purple; some forms have tentacles which are beautifully pigmented. The size varied from species so minute as to almost escape detection up to fine showy forms 1–2 in. in diameter. They form considerable colonies, sometimes covering areas of several square feet. Isolated individuals, particularly of the larger species, are not rare. Usually their rosette of tentacles and brilliant color renders them quite conspicuous, but many kinds are embedded more or less completely in the substratum, and upon the slightest alarm contract into shapeless lumps, and are thus easily overlooked.

FIG. 7. Coral Reefs near Honolulu, Oahu. The city of Honolulu is built upon a limestone plain. The coral reefs which extend along the coast are well developed and very rich in plant and animal life. There are numerous evidences of repeated subsidence and elevation. The crater on the right is Diamond Head (Leahi); the channel to the left is Kalihi Channel. Honolulu Harbor is the middle channel.

The *Ctenophoræ* have about 20 known species in Hawaiian waters, but these are so rare and fragile that they are practically unknown to the reef-collector. They are all pelagic, delicate, transparent creatures, with long tentacles and peculiar comb-like locomotor organs. As they swim gently through the sunlit waters their transparent bodies and tentacles yield beautiful iridescent reflections. *Hormiphora*, *Cestus*, and *Beroë* are well-known genera. All the members of this highly specialized group are solitary and do not form skeletons.

The fauna which inhabits the innumerable small cavities in the coral, and which drills countless tunnels through the soft rock, is of much interest. This fauna comprises chiefly the worm-like animals or sea-worms. Important groups are *Turbellaria, Nemertinea,* and *Annelids.* Some species creep about in the interstices; others construct covered passageways on the surface of the coral. Others burrow in the sand and mud on the floor of the lagoon. Some tunnel deviously through the coral rock itself. Many of the sea-worms are brightly colored. Little is known concerning the relationships or life-histories of the Hawaiian forms. *Nereis, Serpula, Terebella, Tubifex, Sipunculus,* and *Echiurus* are characteristic annelid genera.

The true corallines (*Polyzöa*) or sea-mats bear a close resemblance to the hydroid zoophytes, and only upon microscopic inspection show that their organization is much higher than that of the hydroids. The skeleton is not exclusively calcareous; in many forms it is chitinous or even gelatinous. These corallines are abundant on the Hawaiian reefs.

The true starfishes, *Asterioidea,* are comparatively rare on the reefs themselves, although fairly common in the offshore waters. The brittle-stars, *Ophiuridea,* are the common reef forms, and lurk in every cranny. The *Albatross* expedition collected 60 Hawaiian species of true starfish during its dredging operations in the island channels; they were taken at depths of 60–6,000 ft. These represented 46 genera and 20 families; 52 species were new to science. According to Bryan,

> Large specimens of an eight-rayed starfish, *Luidia hystrix,* are occasionally captured at Pearl Harbor. They are often a foot and a half in diameter. A similar but very small species is to be found abundantly in the coarse green sponges in Kalihi Bay and at Pearl Harbor. A small, stiff, irregularly developed, pink, leather-like species, *Linckia* sp. without spines, is occasionally found crowded into small holes in the coral reef.

The common brittle-star, *Phiœma* sp., is blue-black in color, with small body and long snaky arms. It is gre-

garious in habit, and the collector frequently finds a dozen or more congregated beneath a half-buried stone or coral mass. A tiny pink species, *Ophiothrix* sp., with remarkably long arms, inhabits crevices in the coral. It is very difficult to capture intact, because it, like most of the Ophiuroids, possesses to a remarkable degree the faculty of self-mutilation. Many of the Hawaiian brittle-stars, when disturbed or removed from the water, sever portions of their arms piece by piece until finally nothing is left but the central disc. This is capable of developing a new set of arms; and a detached arm can, under favorable conditions, develop a new disc and a completed series of arms. The basket-stars, *Cladiophiuræ,* have never been collected on the Hawaiian reefs.

The sea-urchins, *Echinoidea,* are richly represented, but most of the species inhabit the deep offshore waters. The inshore species are gregarious and common in all rocky situations along the coasts, as well as on the reefs themselves. *Podophora pedifera,* for example, prefers the black lava rocks and cliffs exposed to the full force of the surf, and is so abundant that the zone of massive basalt which it inhabits is literally honeycombed with its burrows. Several species of *Echinometra* are also very abundant; these prefer the shallow waters of the lagoons. In the deep holes and caverns along the outer edge of the reef is a large purple-black species, *Diadema paucispinum,* with slender, awl-shaped spines. In the same situations occurs *Echinothrix desori,* a large form whose long spines are beautifully banded with gray and black. The curious club-spined urchins, *Heterocentrotes* spp., occur here and there along the reef, and are frequently exhibited in the Honolulu Aquarium. The sea-biscuit, *Brissus carinatus,* is a large, heart-shaped urchin, covered with short, brown hair-like spines, and is occasionally found along the reef rim. A number of the Hawaiian urchins are known to the natives as *wana,* or "sea-eggs," and are habitually used by them for food. They may be purchased in the local fish markets.

Numerous species of holothurians (known as sea-cucumbers, sea-squirts, and *bêche-de-mer*) are common in the shallow waters. There are over 40 described species, representing 4 families and 21 genera. A large, worm-like form, *Opheodesoma spectabilis,* is common at Pearl Harbor and Kaneohe Bay, in quiet water. It is about 2 ft. long and 1½ inch diameter, reddish brown mottled with brown. A large, dark greenish-brown species, *Stichopus tropicalis,* is plentiful in the large pools of the outer reef, near Honolulu. Inhabiting the tidal pools in the lava rocks is another large form, *Holothuria atra;* dark brown, and with ambulacral feet scattered all over its body. Frequently associated with it is a heliotrope-purple species, *Holothuria cinerascens.* There are about 600 known species of holothurians, varying in size from ½ inch to 2 or 3 feet. They are found in all seas, but are particularly abundant in the West Indies, and between Asia and Australia. They feed chiefly on Foraminifera. The movements of all the Hawaiian species are very sluggish; they seem to have few enemies. All are harmless, although of unpleasant aspect. They are capable of the most extraordinary regeneration of parts, even of the most important organs. Many species show the curious habit of evisceration—when alarmed they dispel from the anal opening the viscera either wholly or in part. In the course of a few weeks all of the lost organs are replaced by a new set.

The Crinoids or sea-lilies do not exist in the shallow waters of the Hawaiian reefs. A dozen forms were collected by the *Albatross* at depths of about 600 ft. These all proved to be new species, although representing 8 wide-ranging genera in 4 families of the non-stalked *Neo-Crinoidea.* Crinoidal fossils have not been found in the uplifted coral limestone beds of the Hawaiian Archipelago. These forms made important contributions to the Silurian and Devonian rock strata in other parts of the world, during which epochs the crinoids were enormously abundant.

Molluscs abound on all the reefs. There is a tremendous range of size, structure, habitat and generic representation. The marine molluscan fauna has never received adequate attention, as scientific interest has centered upon the unique terrestrial and arboreal forms. There are about 20 species of bivalves (*Pelecypoda*) that are fairly common. These include such genera as *Mytilus, Perna, Arca, Ostrea, Anomia, Pecten, Tellina, Cadokia, Cytherea, Venus, Cardium* and *Chama*. *Tellina sugosa,* the *Olepe,* is, according to Bryan, "the most important shell-bearing mollusc" in the islands. The famous pearl shell, *Avicula margaritifera,* of the South Pacific, does not occur in Hawaiian waters. The Hawaiian pearl oyster, *pa, Margaritifera fimbriata,* has a shell often 3 or 4 inches broad, with a brilliant iridescent interior. It is the species which gave Pearl Harbor its name. In the early days the collecting of *pa* was a royal monopoly, like the collecting of sandalwood. The pearl-shell was used by the Hawaiians chiefly for making fish-hooks, and for the curious shell-eyes of their wooden gods. A true pearl-bearing species also occurs at Pearl Harbor and other localities in the group in the deeper offshore waters. The edible oysters are represented by *Ostrea rosea,* which is not of sufficient abundance to permit commercial exploitation.

The chitons and their allies, *Amphineura,* are uncommon in the shallows, but a thorough systematic survey would undoubtedly bring to light many additional forms. The true chitons, *Placophora,* are confined largely to the shallows, and apparently are herbivorous, feeding on minute algæ and diatoms. The *Aplacophora* as worm-like, shell-less creatures, with the body beset with calcareous spicules. They are wholly absent from the littoral zone, occurring only at considerable depths—3,000 ft. and in some instances down to 7,500 ft. They are carnivorous and subsist on such small animals as hydroids and coral polyps.

The univalves or Gasteropods are by far the most

abundant molluscs on the Hawaiian reefs and aggregate several hundred species. Space forbids any detailed treatment of this huge and highly diversified class. A bare enumeration of important and common families and genera, adapted from Bryan, will indicate the richness of the marine univalve fauna (the number of species is in each instance an approximation):

Family	Species	Typical Genera
Tritons; Tritonidæ	12	*Triton, Ranella.*
Spiny Rock Shells; Muricidæ	30	*Purpura, Ricinula, Vexilla, Sistrum.*
Spindle Shells; Fusidæ	6	*Fusus, Latirus, Peristernia.*
Whelks; Buccinidæ	6	*Pisania, Cantharus.*
Dog Whelks; Nassidæ	4	*Nassa.*
Mitre Shells; Mitridæ	26	*Mitra, Imbricaria, Turricula.*
Margin Shells; Marginellidæ	4	*Erato, Marginella.*
Olive Shells; Olividæ	4	*Harpa, Oliva.*
Dove Shells; Columbellidæ	15	*Columbella, Engina.*
Cone Shells; Conidæ	25	*Conus.*
Auger Shells; Terebridæ	25	*Terebra.*
Conch Shells; Strombidæ	9	*Strombus.*
Cowry Shells; Cypræidæ	40	*Cypræa, Trivia.*
Tun Shells; Doliidæ	2	*Dolium.*
Cameo Shells; Cassisæ	5	*Cassis.*
Moon Shells; Naticidæ	10	*Natica.*
Slipper Shells; Calypræidæ	12	*Crepidula, Crucibulum, Hipponyx.*
Eulimas; Eulimidæ	17	*Eulima.*
Pyramid Shells; Pyramidellidæ.	3	*Pyramidella.*
Sun-dial Shells; Solariidæ	6	*Solarium.*
Violet Snails; Ianthinidæ	3	*Ianthina.*
Ladder Shells; Scalariidæ	10	*Scalaria.*
Herald's-horn Shells; Cerithiidæ	20	*Cerithium.*
Periwinkles; Littorinidæ	3	*Littorina, Modulus, Risella.*
Sea-Snails; Neritidæ	10	*Nerita, Neritina.*
Turban Shells; Turbinidæ	18	*Turbo, Phasianella, Astralium.*
Top Shells; Trochidæ	12	*Trochus.*
Limpets; Fissurellidæ and Patellidæ	10	*Helcioniscus.*
Sea Slugs; Nudibranchiata	10	*Aplysia.*

The highest and most highly specialized class of molluscs, the Cephalopods, have an abundant and familiar representative on our reefs, in the form of the common octopus or *he'e.* This is popularly called "squid" although it is a true cuttlefish, with a small round sac-like body and eight arms. It is very common in holes and

pools on the rocky platform of the reef, and in caverns along the reef-rim. During the day it hides in cavities; at night it creeps about over the rocks of the bottom. The natives are very fond of the flesh, which they prepare for food in a variety of forms. Dried "squid" is common in the fish-markets. Our cuttlefish is rarely more than 18–26 inches in length. The true "devil-fish" of many a sea-tale is a giant squid, *Architeuthis,* which inhabits the Newfoundland banks and often attains the gigantic proportions of an over-all length of 50 ft., with a body 6 by 9 ft., and enormous arms 40 ft. long.

Fig. 8. Coral Reefs near Pearl Harbor, Oahu. The inlet to Pearl Harbor is shown to the right. To the left is the southwest point (Barber's Point) of the island. The lowland is a plain of coral limestone; the reef is rich in biological material.

Our reefs support a characteristic crustacean fauna. In the growing coral at the reef-edge are found a number of small Cyclometopous crabs, which are often beautifully sculptured and colored to harmonize with the coral. The *Alpheidæ,* which are shrimp-like *Macrura* with highly asymmetrical claws, are commonly found in pools on the reef. In the coral rubble formed by the disintegration of the reef-rim, in relatively shallow water, numerous Leucosiid crabs are found. Many lowly forms of Entomostraca are abundant, but have never been surveyed

taxonomically. The Phyllopods, Ostracods and Copepods are all plentiful. The Cirripedia include the most aberrant of the crustaceans, and are represented by the common barnacles, including both the stalked (Lepadidæ) or goose barnacles, and the sessile (Balanidæ) or acorn-

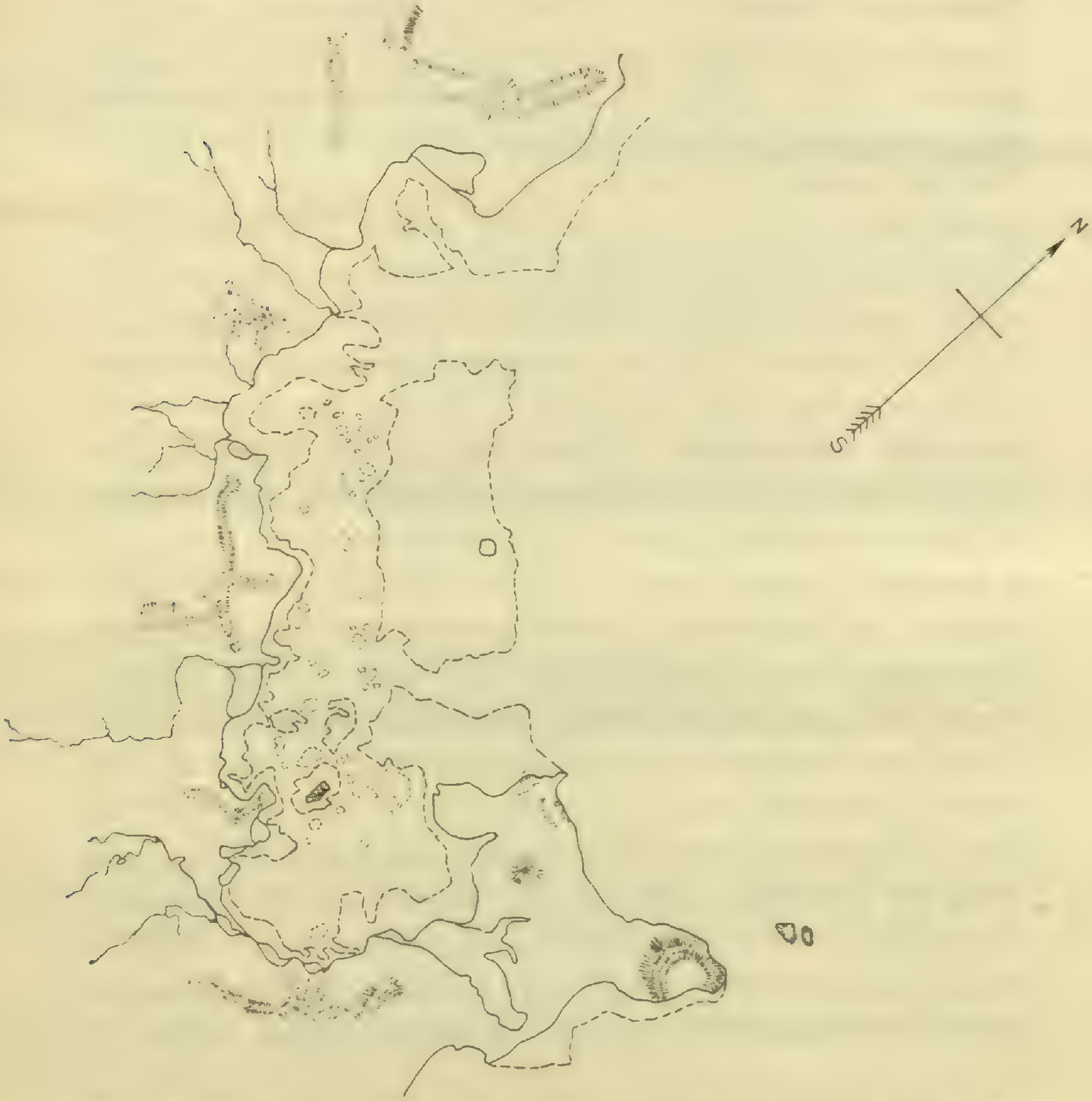

FIG. 9. Kane-ohe Bay, Oahu. This bay, which is a drowned valley complex, has a great variety of coral formations. There are many small coral isles and atolls; some are of notable perfection. The exact boundaries of the outer reefs are not known. The crater and little isles to the lower right are secondary volcanic products.

shells. The latter are exceedingly abundant along the shores and reefs; there are also numerous deep-water barnacles.

The most commonly known, the largest and the most highly organized crustaceans, the Malacostraca, are very common. Space does not permit even a general sketch of the many crabs, prawns, crayfish and other interesting forms that teem in the Hawaiian littoral. The so-called Hawaiian "lobster," *ula, Panulirus japonicus,* is really a large marine crayfish, and not closely related to the true lobster. It is brilliantly colored and ornamented, with spiny carapace and long antennæ. The *ulà* is common in the fish markets, as are also species of *Scyllarides, Ocypoda,* and many crabs. Hermit crabs (*Onomura*) are common and in great variety. They make their homes in empty sea-shells, and have many interesting habits.[6]

The last great division of the reef fauna comprises the fishes, a group that could easily occupy the space of an extended monograph. There are several hundred reef species, occupying a wide range of habitats, and varying in size from minute species up to huge food-fish weighing a hundred pounds each. Like the fish of many tropical waters, the Hawaiian species are famous for their brilliant coloration, fantastic patterns, and strange shapes. Many are grotesque; many are exceedingly beautiful; many are consummate embodiment of that riot of gorgeous color that is so characteristic of the reef and its life. The reef fishes, like the other littoral forms of life, were an important item in the dietary of the primitive Hawaiians, and continue so to the present day. Most of the common species are offered for sale in the fish-markets. Space is not available for any detailed account of the in-

[6] The following list of common littoral and reef species and genera of malacostraceans will indicate the richness of this portion of Hawaii's remarkable reef fauna: I. Brachyura—*Ocypode ceratophthalma, O. lævis, Grapsus grapsus, Metopgrapsus messor, Pachygrapsus plicatus, Cyclograpsus, Percnon, Carpilius, Platypodia, Lophozozymus, Xantho, Leptodius, Xanthodius, Etisus, Actæa, Chlorodiella, Phymodius, Grapsillus ferrugineus, Polydectus cupulifer, Portunus, Charybdis, Thalamita, Podophthalmus, Simocarcinus simplex, Calappa;* II. Macrura—*Scyllarides, Patæmonella, Parribacus, Panulirus, Stenopus, Penæus, Hippolysmata, Spirontocaris,*

shore[7] fishes, as contrasted with the pelagic and abyssal species.

[7] Some of the more important groups and species may be listed as follows:

Sharks	*Carcharias melanopterus; C. nesiotes; Sphyrna zygæna; Isuropsis glauca.*
Rays	*Stoasodon narinari.*
Tarpons	*Elops saurus.*
Bonefishes	*Albula vulpes.*
Milkfishes	*Chanos chanos.*
Anchovies	*Anchovia purpurea.*
Lizardfishes	*Trachinocephalus myops; Synodus varius; Saurida gracilis.*
Conger Eels	*Leptocephalus marginatus.*
Morays	*Muræna, Enchelynassa, Gymnothorax, Eurymyctera, Echidna, Uropterygius, Scuticaria.*
Trumpetfishes	*Aulostomus valentini.*
Cornetfishes	*Fistularia petimba.*
Needlefishes	*Athlennes hians.*
Half-beaks	*Hemiramphus depauperatus; Euleptorhamphus longirostris.*
Flyingfishes	*Parexocœtus brachypterus; Cypsilurus simus; C. bahaiensis.*
Friars	*Atherina insularum.*
Mullets	*Mugil cephalus.*
Barracudas	*Sphyræna helleri.*
Threadfins	*Polydactylus sexfilis.*
Squirrelfishes	*Holotrachys lima; Myripristis* spp.; *Flammeo sammara; F. scythrops; Holocentrus* spp.
Big-eyed Scads	*Trachurops crumenophthalma; Carangus.*
Threadfishes	*Alectis ciliaris.*
Cardinalfishes	*Mionorus, Foa, Amia.*
Groupers	*Epinephelus quernus.*
Catalufas	*Priacanthus.*
Snappers	*Apsilus, Aphareus, Bowersia, Aprion, Etelis.*
Porgies	*Monotaxis grandiculis.*
Rudderfishes	*Kyphosus.*
Surmullets	*Mulloides.*
Goatfishes	*Pseudupeneus; Upeneus.*
Demoiselles	*Dascyllus; Chromis; Pomacentrus; Abudefduf.*
Wrassefishes	*Lepidaplois; Stethojulis; Halichoeres; Gomphosus; Anampses; Thalassoma; Julis; Coris; Cheilio; Cheilinus; Novaculichthys; Iniistius; Hemipteronotus; Xyrichthys.*
Scarids	*Calotomus; Callyodon.*
Butterflyfishes	*Forcipiger; Chætodon; Holocanthus.*
Moorish Idols	*Zanclus canescens.*
Surgeonfishes	*Hepatus, Zebrasoma, Ctenochætus, Acanthurus, Callicanthus.*

The gorgeous colors of many of our reef fishes are very evanescent, and undergo rapid deterioration when the fish is taken from the water. Hence the coloration of those offered for sale in the markets often conveys but little idea of their living hues. Preserved specimens and printed descriptions are of even less value.

In concluding this condensed sketch of the Hawaiian reefs, the writer desires to emphasize his impression of the struggle for life which goes on there unceasingly. The reef is a region of intense competition. It is comparable in many of its ecologic relations to the montane rain-forest. The excessive illumination of the reef is perhaps as constraining an influence as is the excessive humidity of the rain-forest. The diversity of organisms which inhabit the reef is far greater than that of any other island habitat. The competition for food is keen and unremittent.

The reef as a food supply for human beings has been a dominant factor in the lives of the primitive Polynesians. Through the experiences of thousands of years they have acquired a very intimate knowledge of the reef and its life, but this has never been given adequate scientific investigation. One of the great forward steps in the economic history of the world will be the scientific utilization of coral reefs and their products.

Triggerfishes	*Balistes, Balistapus, Stephanolepis.*
Puffers	*Tetraodon, Canthigaster.*
Trunkfishes	*Ostracion, Lactonia.*
Cirrhitoid fishes	*Paracirrhites, Cirrhites.*
Mail-cheeked fishes	*Caracanthus.*
Scorpænids	*Sebastapistes, Sebastopsis, Scorpænopsis.*
Gobies	*Eleotris sandwicensis, Asterropteryx semipunctatus, Eviota epiphanus, Gobiomorphus eugenius, Mapo fuscus, Gobiichthys, Gnatholepis knighti.*
Blennies	*Enneapterygius atriceps, Alticus, Enchelyurus, Salarias.*

CONTINUOUS AND DISCONTINUOUS VARIATIONS AND THEIR INHERITANCE IN PEROMYSCUS. III

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VII. MUTATIONS

In a recent paper (1917*a*) I have described two widely aberrant color types which have appeared in my cultures, together with certain minor deviations, which likewise seem to behave as discontinuous variations. I am prepared to add considerably to the data thus far published.

1. "*Partial albinos*"

The term albino, as applied to these mice, admittedly does not conform to current usage, and this has become especially evident with the appearance of the mature pelage. I do not think, however, that any of the various names given to fancy races of *Mus musculus* apply to these animals. Having at hand no specimens or even satisfactory colored plates of fancy mice, I am unable to make the comparisons.[27] As previously stated, this mutant strain has red eyes, and lacks pigment wholly on the ears and tail. The fur, on the colored region of the body, is a very pale gray, rather strongly tinged with a shade of yellow approaching Ridgway's "ochraceous buff," or perhaps "ochraceous orange," on the most highly colored areas. As a convenient non-committal expression, I shall henceforth employ the term "pallid" for these mice."

A microscopic examination of the hairs of these mice reveals some interesting departures from the normal condition:[28] (1) a considerable proportion of the hairs are practically devoid of pigment in the zone which is ordinarily yellow, while the rest are normal in this respect;

[27] It may be that the factional modifications of my mice are the same as those of Castle's "red-eyed yellow" rats (see Castle and Wright, 1915).

[28] Cf. Morgan's account (1911) of the hair of some "modified" individuals of *Peromyscus leucopus ammodytes.*

(2) the surface pigment of the terminal portion of the hairs is nearly or quite lacking; (3) in the basal zone, the black pigment bodies are represented by small flocculent dark masses. Thus, we are not, as in the next "mutant" to be described, merely dealing with changed proportions of perfectly normal types of hair. These red-eyed mice possess types which I have not found in any of the rest of my stock.

At the time of my earlier description of these pale sports, no young had been obtained, but their pedigree suggested that they were simple Mendelian recessives. This conjecture has thus far been sustained. The two "mutants," bred to one another, have given six pale young, like themselves, and no others. When bred to dark mates, of the same stock as themselves (*sonoriensis-rubidus* hybrids), the pallid animals gave only dark young, except in a single instance where the dark parent was known to be heterozygous. In this case, one pallid mouse was the outcome. Of the dark progeny, three broods, aggregating eleven individuals, have thus far been born.

This clear-cut and typical example of Mendelian segregation, in respect to these *mutant* characters, is in striking contrast to the complete lack of segregation—so far as is obvious—in respect to the *subspecific* characters which have entered into the germinal constitution of these same individuals.

As I have previously stated, these parent "mutants" were the offspring of F_1 *sonoriensis-rubidus* hybrids. In a recent article (1917) the Hagedoorns have described a number of strongly aberrant types of rats (including some waltzers!) which appeared in a mongrel strain resulting from the crossing of *Mus alexandrinus, M. tectorum* and *M. rattus*. The authors recognize in these aberrant derivations some entirely new products, though they do not attribute their origin to real mutation. In the opinion of the Hagedoorns, as I understand it, these apparently "mutant" characters have resulted, in each case, from the chance coming together of two recessive factors (or two "absences," according to the prevailing

theory). No two of these "absences" coexisted in the gametes of any one of the parent species, and no single "absence" by itself is believed to be adequate to produce one of the abnormalities. Since the average number of each kind of "mutant" in their stock of 37 was approximately 1 in 16, they assert:

> These numbers make it clear that we are not dealing with a sort of period of mutation; it was easy to see that the new types were already given in the genotype of the three species crossed (p. 415).

And in later passages the authors generalize this conjecture, as for example:

> The only cause for inheritable variability in multicellular organisms which can be of any account in evolution is mating between individuals of unequal genotype, crossing in the widest sense (Amphimixis) (p. 418).

That the Hagedoorns's explanation does not fit the case of my pallid *Peromyscus* is evident from the history of the stock. I have obtained, in all, 47 F_2 offspring from the mating of F_1 *sonoriensis-rubidus* hybrids, counting only those animals which lived long enough to reveal their essential color characters. These were the progeny of six different fathers and eleven different mothers. Just four of these very pale sports have appeared in my F_2 stock. They are the offspring of a single father by two mothers, both his own sisters. These mothers, by the same father, also produced seven dark young.

It seems plain, therefore, that the mutation in question is not due to any recombination of factors (or their "absences") regularly occurring in the parent races. If it were, we should reasonably have expected similar aberrations among the offspring of other parents. It is hard to determine from their published statement the exact pedigree of the Hagedoorn's aberrant rats. But one thing seems plain. All were the progeny of a single father by two mothers, the latter apparently being sisters. The authors are certainly not warranted, therefore, in assuming that such results would have been obtained by mating *any* animals of the same racial composition.

I am inclined to think that my pale red-eyed mice are true mutants, *i. e.*, that they appeared *de novo* in my cul-

tures. It is more than possible, likewise, that the hybridization of such diverse strains was the disturbing element that led to the loss or modification of a "gene." The latter possibility is strengthened by a consideration of the Hagedoorns's waltzing rats and abnormalities of coat color. But this is a very different view from the hypothesis that "the new types were already given in the genotype of the . . . species crossed."

2. *Yellow gambeli*

The five normally colored progeny of a single pair of normally colored *Peromyscus maniculatus gambeli* (La Jolla race) became the parents of 21 offspring, of which 14 were normally colored and 7 were of a peculiar yellowish-brown color. These "mutants," which I have called "yellows," are of a shade not very far removed from Ridgway's "clay color." They are considerably darker than some, at least, of the yellow races of *Mus musculus.* Microscopic examination of the hair of these aberrant *gambeli* shows that it is closely similar to that found upon the more highly colored parts of *P. m. sonoriensis.* In comparison with normal specimens of its subspecies the mutant strain is found to have a larger number of the yellow-banded hairs, in proportion to those which are black throughout their entire length. The latter type of hair is, however, by no means wanting. In the second place, the yellow zone of each hair, on the colored parts of the body, occupies, on the average, a considerably larger proportion of its length. On the midventral surface, the basal, plumbeous zone is quite lacking, the hairs being entirely white. Besides the differences stated, I can not be certain of any hair characters which distinguish this type of sports from the normal stock. Moreover, the eyes, ears, tail, etc., carry a normal amount of black pigment.

It is to be noted that these "yellow" mice, unlike the "partial albinos," are not distinguished by any types of hair which are lacking in normal individuals. We may, however, very justly regard the yellow condition as having arisen through "discontinuous variation." Though due

merely to a change in the proportion of elements previously present, the new type has arisen abruptly and has diverged so widely that its range of variation does not overlap that of the normal race. Among the many hundreds of individuals which I have dealt with, I have never found any mice which would serve in a true sense to bridge the gap between these two types. Nor have any other yellows appeared in my cultures, except among the descendants of the single pair in question.[29]

As stated in an earlier paper (1917*a*), I trapped several years ago a mouse which I feel fairly certain was a juvenile yellow *gambeli.* It is possible that this character, in a heterozygous condition, may be of not uncommon occurrence among the mice of this vicinity. Thus, the mutation through which my stock came into existence may have taken place among the wild ancestors, many generations earlier. On the other hand, the same genetic instability which led to such a factorial loss or modification in one case may be responsible for its occurrence on many independent occasions. I have no data by which to decide between these two alternatives.

As regards the genetic behavior of these yellow mice, I have fairly satisfactory evidence that they are simple Mendelian recessives. As was stated above, 7 yellows and 14 normal animals constituted the fraternities in which they first appeared. The departure from Mendelian expectation may well have been accidental here, though a differential mortality may possibly have been responsible. The first yellows, bred to their (presumably heterozygous) parents, have given 5 dark and 5 yellow offspring. Bred to homozygous dark animals, they have thus far produced only a single brood, consisting of three dark individuals. Yellows bred to yellows have produced young of the aberrant type only (thus far 10). These frequently do not attain the full yellow color until they as-

[29] Mr. H. H. Collins has, however, found a number of sports of this general appearance among the offspring of a single pair of normally colored individuals which were trapped at La Jolla. Mr. Collins' mice differ somewhat in shade, however, from my "yellows," and may represent a distinct "mutation." His experiments have not been carried far enough to test the genetic behavior of this character.

sume the mature pelage, but I no longer have reason to doubt that the yellow type "breeds true."

A yellow female *gambeli* mated to a "pallid" male of the strain discussed above, has given birth to a single offspring, having abundant dark pigment in the skin, eyes and hair. In other words, these two pale, recessive mutants seem to be "complementary" to one another, as were Castle's two yellow races of rats (Castle and Wright, 1915).

3. *Discontinuous Variation in Restricted Pigment Areas.*

I have discussed briefly elsewhere several sorts of color markings, along with limited data which seemed to show that some of these were inherited in alternative fashion. Other characters of the same type have been added to the list. For example, in the second cage-born generation of *gambeli* I have found three mice with faces strongly "grizzled" by the presence of white hairs. It is probably no mere coincidence that these three grizzled specimens, while not belonging to a single fraternity, are all descended from the same grandparents. Neither the parents nor the grandparents were recorded as having the peculiarity in question, which would hardly have been overlooked if present. Furthermore, the single offspring which I have obtained from a "grizzled" pair exhibits this character plainly, though in a reduced degree. One specimen showing the white-faced condition likewise appeared in the C_2 generation of *sonoriensis.*

Again, occasional mice of perhaps all of the races are characterized by having considerable pigment in the skin of the tail. Normally, the skin of this member is nearly or quite devoid of pigment, the dorsal tail-stripe being due to black hairs. Examination of two successive generations of *rubidus* makes it probable that this caudal skin pigmentation is likewise a hereditary character.

I shall here discuss only one of the localized pigment variations which were dealt with in my earlier report on color "mutations." This is the occurrence of a white-tipped snout, due partly to the absence of skin pigment and partly to the presence in this region of white hairs.

I am now able to indicate rather more definitely the mode of transmission of this character. I wish to lay some stress here upon its genetic behavior, since I regard it as an interesting case in its bearings upon certain theoretical questions.

The pale-nosed condition has been studied only in the darkest of my races, *rubidus*. It was not noticed in the original wild stock, but it may well have been overlooked, as it is not a conspicuous character, and I was not searching for this type of variations when the wild generation was examined. In the first cage-born ("C_1") generation twelve mice were recorded as having white-tipped snouts, four of the cases being entered as doubtful. At the time of examining these animals I had no idea as to the parentage of the individuals, so that there was no bias in my selection. Upon looking up their pedigrees, I found that ten of the twelve cases (eight certain and two doubtful) were the offspring (indeed, the *only* offspring) of two mothers of the wild generation (P ♀ 40 and 41) by a single father (P ♂ 15). The other two cases (both doubtful) were of other parentage. In connection with the figures just given, it must be stated that the C_1 generation consisted altogether of 60 (surviving) individuals, these being the progeny of twelve females and nine males.

Only 38 mice were obtained in the C_2 generation, 6 of which had white-tipped snouts. As before, the count was made without my being aware of the parentage of the individuals examined. Of the six "mutants," it turned out that four belonged to a fraternity of five, the fifth member of which was normal. This fraternity was the offspring of C_1 ♀ 61 (normal) by C_1 ♂ 10 (white-nosed). The other two mutants were the offspring of this same C_1 ♀ 61, by one of her brothers (♂ 3), the latter being likewise normally pigmented. These parent animals we may believe to have been heterozygous.

Unfortunately, none of the matings of the pale-nosed C_1 individuals *inter se* proved fertile, and indeed the only one of these aberrant mice which left descendants was the ♂ 10 referred to above.

The relationships here indicated, and the incidence of

the aberrant condition, are quite intelligible on the assumption that we have to do with a monohybrid recessive character. The character can not be dominant, for we had a case of white-nosed young from two dark-nosed parents. It can not well be due to more than one factor, owing to the relatively large number of recessive individuals.

VIII. Discussion

Any one approaching the data dealt with in the foregoing pages, unhampered by theoretical considerations, would, I think, conclude that we had to do with two types of variation and two types of inheritance, differing from one another in rather fundamental ways. In the one class we have the continuously graduated differences, occurring within the limits of one of our "subspecies," as well as the differences in average or modal condition which distinguish the various subspecies from one another. Here we find a sensible *continuity*, both within and between these rather artificial assemblages of individuals, and distinct taxonomic units can be recognized only if we erect more or less arbitrary boundaries. In heredity, likewise, we have no indication of a dominance of one step or grade in this series over another, and little to suggest that two of these grades, once united or blended in the offspring, tend to reassert their independence in subsequent generations.

In the other class we have the "sports" or "mutations." These are distinctly *discontinuous*, in relation to the parent stock, either in the sense that one of the two possesses elements which are altogether lacking in the other, or at least in the sense that the new form has undergone such a change in the proportions of existing elements that its range of variation does not overlap that of the normal race. Looked at in another light, it is of interest to note that all the mutations which I have discussed, with a single exception, are dependent upon the loss of something. The red-eyed "pallid" mice have lost most of their black and some of their yellow pigment, the "yellows" have lost much of their black. The white-tipped tails are due to a loss of part of the dorsal tail-stripe, the

"grizzled" heads likewise to the local loss of hair pigment, while the white snouts have resulted from a loss of pigment both in the skin and hair of the latter region. The single exception among the "mutations" which I have observed in *Peromyscus* is the occasional presence of skin pigment in the tail. Here something has been definitely added to the usual condition.[30]

In heredity, too, these mutant characters, whether negative or positive, behave in distinctly discontinuous fashion. They do not blend, but are either present or absent in their entirety.

Taken at face value, I say, the evidence shows that we have to do here with two different types of variation and two different types of heredity. Now admittedly, the naïve view of such a situation is not necessarily the correct one, else we should be forced to return to the geocentric theory of the solar system. But even in this last instance, the burden of proof most assuredly rested on the man who first asserted that the sun did not move around the earth. And to-day the same burden rests upon those who claim—possibly with truth—that heritable variations are all discontinuous and that blended inheritance is an illusion.

In the few remaining pages of this paper, it is obviously impossible to discuss the various lines of evidence which have been advanced in favor of the Mendelian-mutation-pure-line scheme of things. I think that few would be enthusiastic enough to assert that the case had yet been really proved on evidential grounds. The considerations which are chiefly effective in determining one's adherence to this system of beliefs are doubtless of a more general nature. Thus it is argued that Mendelian inheritance has been shown to hold rigidly throughout a vast range of material, and that, therefore, the "unit-factor" conception is probably of universal application. Or, it is contended that the scheme of things here considered is more

[30] Even in this case, it is possible that we have to do merely with a "reversion," or return to an ancestral condition. Some other Muridæ (*e. g.*, *Mus musculus*) normally have abundant pigment throughout the skin of their tails.

in harmony with the atomistic principles of physics and chemistry. "Unit-factors" have even been identified with molecules.

In respect to the pigmental characters of our geographic races, it has been shown to be probable that insensible gradations occur throughout considerable ranges of territory. There results a series in which marked contrasts can be found only by comparing individuals from widely separated localities. The hypothesis that the variations in this case are of the Mendelian type involves the assumption that the subspecific differences have arisen by a whole succession of small mutations in the same direction, the number of these mutations being a function of the distance from some hypothetical center of dispersal. In a recent paper (1917) Morgan has considered the question whether there are "any connections between the gradations of character in allelomorphic series and the order in which the characters appear," *i. e.*, whether "the assumed fluctuation of factors is a sequential process." He concludes that, "as a matter of fact, there is no such relation known . . . for the actual evidence from multiple allelomorphs shows that genes may mutate in all directions and also that extreme mutations such as white eyes arise suddenly from red and not by graded steps" (p. 524). These assertions, which, it is true, were primarily concerned with the effects of selection, lend little support to the view that graded geographic variations have arisen through mutation.

The attempt to explain away the substantial mass of evidence for permanent gametic blending and the indefinite efficacy of selection by invoking the theory of "multiple factors" is too well known to be reviewed here. Castle has been the most able and vigorous opponent of this theory. At present I will merely refer to certain evidence of my own which, I think, supports such an explanation no better than Castle's.

The dorsal tail-stripe is entirely lacking in a certain strain of my mutants. This stripeless condition is recessive to the striped one. In crosses with normal mice, the

stripe appears in its full size and intensity.[31] Nevertheless, the stripe itself was shown in the preceding pages to vary from race to race and from one individual to another. *And these variations, both racial and individual, were found to be hereditary.*

The case, of course, is parallel to that of Castle's hooded rats. Since "hoodedness" is recessive to "self-color" and reappears in one fourth of the F_2 generation, Castle argues that it is dependent upon a single unit factor. Nevertheless, this factor itself presents hereditary variations in "potency," since it can be modified indefinitely by selection. The Mendelian counter-argument is that "hoodedness" behaves as a unit character in certain crosses merely because there is some one factor without which it can not manifest itself *at all.* The variability in its *degree of manifestation* is due to the fact that the hooded pattern is modified by the action of a number of independent cumulative factors. The argument seems a bit scholastic, but we must admit that it is logical and consistent.

Take another instance. Here I admit that my evidence is to some extent inferential at present. I have given good grounds for believing that the pigmentless condition of the snout in certain strains of *rubidus* is a simple recessive trait, dependent upon a single factor (or its absence). By this I mean that the pigmentless condition is probably allelomorphic to *any degree of pigmentation whatever.*

Now we find, in examining a series of mice, all gradations from those with heavily pigmented snouts to those in which no pigment is to be discovered with the aid of a hand lens. Indeed, there are a few "borderland" cases, which can be only doubtfully distinguished as pigmented or unpigmented. Unfortunately, I have no data showing whether or not these various gradations are hereditary. Analogy with the case of the tail-stripe would make it probable that they are. Moreover, we do know that those

[31] The fact that this condition of the tail stripe is but one manifestation of a mutation which has affected the hair pigment of the entire body does not affect the argument. It is generally believed that most "unit factors" manifest themselves in diverse ways.

differences in the mean condition of the snout which distinguish the various local races from one another are hereditary.

Here, too, I am aware that we could argue, with flawless logic, that the pigmentless condition was due to the dropping out of some single factor, without which the formation of snout pigment in *any* quantity was impossible. Each member of the graded series of pigmented snouts we might suppose to be conditioned by the presence of this color factor, together with one to many cumulative factors determining the degree of its manifestation.

Johannsen (1913), Morgan (1915) and others have made much of the increased range of variability which has frequently been met with in the F_2 and subsequent generations, even when appearances otherwise pointed to a permanent blending of types. Recently several writers, particularly MacDowell (1916) and Little (1917), have analyzed some of Castle's data and have reached conclusions directly opposed to his. All of these authors (Castle excepted) hold that increasing range of variability in successive hybrid generations is strong evidence for the hypothesis of multiple factors, and we must grant that a pretty good case can be made out along these lines. The theory runs smoothly until we encounter the awkward class of facts which Johannsen has called by the name of "transgressive splitting," *i. e.*, the ultimate extension of the range of hybrid variability beyond that of both of the parent races combined. These facts would seem to prove too much, despite the ingenious explanation which has been offered by the pan-Mendelians to account for them.

An analysis of my quite limited data furnishes no evidence of an increased variability in the F_2 generation, except where it pretty plainly results from an increase in the amount of actual abnormality, due to the conditions of captivity. In the largest, as well as the most normal of the series, the range of variation actually diminishes when we pass from the F_1 to the F_2 generation. I do not, however, offer the present evidence as conclusive, even for the single case of subspecific hybridization in *Peromyscus*. It should be confirmed by data derived from

more extensive series, consisting of animals which are free from any pathological modifications.

We must urge in passing, however, that evidence of segregation, even if valid, is not necessarily to be accepted as evidence of *complete* segregation. There is no reason why we might not have *partial* segregation, combined with partial gametic blending, as Castle maintains.

In two recent illuminating articles (1917, 1917*a*), Jennings points out how Mendelian-mutationists of the most extreme school have been driven by their own researches into a position that does not differ, according to any pragmatic test, from the one which they so long have vehemently opposed. More and ever more minute hereditary differences in the manifestation of a given character are recognized, until the limit of distinguishability is approached. This state of affairs has been attributed to two causes: (1) hereditary modifications in the constitution of single factors, resulting in the formation of series of gradations, allelomorphic to one another; and (2) the existence of series of independent modifying factors, cumulative in their effects.

As remarked earlier in this paper, the contest has latterly come to resemble that allegorical one of the two knights, fighting upon the opposite sides of the same bicolored shield. And yet there would seem to be a difference. The two knights in the legend were both equally right. In the present case, if we may judge by every pragmatic consideration, the larger measure of right belongs to those who have contended for the frequent permanent blending of hereditary characters in crossing and the continuous modifiability of these characters through selection. The finely spun theories of their opponents may help us to symbolize the machinery underlying these phenomena, but the phenomena themselves, and not the theories, are the indubitable realities in the case.

IX. Summary

1. In the preceding pages, the differences, structural and pigmental, which distinguish four geographical races of deer-mice are discussed in some detail. The pigmental

differences relate to a considerable range of more or less independently varying characters, affecting both the intensity and the extensity of the pigment in the hair and skin. They are found to be, in a general way, correlated with certain elements of the physical environment, while the structural differences do not appear to be so correlated.

2. All of these differences, structural and pigmental, are found to be differences of degree, revealed through a comparison of mean or modal conditions rather than of individual animals. In comparing the less divergent of these races with one another, the frequency polygons for any given character overlap broadly.

3. These subspecific differences, and even the minor differences which distinguish one narrowly localized subrace from the parent form, are found to be hereditary, as evidenced by their persistence when environmental conditions are interchanged.

4. The gradations in certain of these characters by which individuals of the same race differ from one another are found to be strongly hereditary.

5. Hybrids between even the most divergent of these four races are predominantly intermediate in character, both in the F_1 and the F_2 generations. In both of these generations a wide range of variability is exhibited, which, however, is little if any greater in the F_2 than in the F_1.

6. In contrast to the sensibly continuous variation and sensibly blended inheritance shown in respect to these subspecific characters, is the behavior of certain "mutations." Here we meet with typical discontinuous variation, and inheritance of the strictly alternative or Mendelian type. It is insisted that the burden of proof rests upon those who contend that these two types of variation and inheritance are reducible to a single category, that of discontinuity. Anything like a proof of this contention appears to be thus far lacking.

Supplementary Note (July 23, 1918).

It gives me pleasure to call attention to points of close similarity between certain of the views expressed in the

foregoing pages and ones which have recently been advanced by Gates (1917) and by Goldschmidt (1918); likewise to the resemblance between some of the features of geographic variation which I have described for *Peromyscus* and those which have been observed by Swarth (1918) for certain birds. None of these articles had been published at the time the present paper was written.

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JOAN BAPTISTA PORTA

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LIKE a cemetery with costly monuments for the rich, modest wooden crosses for the poor, and for others sites unmarked, hidden beneath brambles and weeds, a picture of death and oblivion—so history of botany has dealt with records of the past, with life and labors crowned with success or hopelessly ignored and forgotten.

For years, nay centuries unchallenged some works have braved the everchanging hands of time, guiding human thought into a highway with increasing light, confronting nature, its laws and problems; great steps have been taken forwards, new facts have been born, militating against former, old conceptions and resulting in complete revolution. Coupled with intense sincerity great skill has conquered, paving the way for future research, culminating in success, or suddenly, without a warning, crushed with defeat. Many a brilliant thought, but disguised by a less powerful style, has remained obscure and unnoticed, until at some proper time, as if surviving itself, it has arisen and gained due homage, even though late and in foreign soil.

Inclement fate has doomed to silence names of great men, more fortunate thus than labors of merit that have been misunderstood, carelessly weighed, and exposed in unfavorable light. Who knows Porta? His work was soon forgotten and in history it stands among those ridiculed or silently passed by. He was born in classic Italy, in the middle of the sixteenth century, an era of scientific research, marked by rapidly increasing interest in botany, with splendid results laid down in precious volumes, copiously and carefully illustrated. They were the days of Cæsalpino, Dodonæus, Conrad Gesner, Fuchs, Clusius,

Lobelius, Caspar Bauhin, all workers in botany, seeking the same source for solving the problems of the plant world, through demonstrating the relations between the plants themselves, and beginning with classification first of all. At that time literature was less than scant; there was actually nothing to distract the views of investigators; it was an era of thought original, with room only for the gifted and talented, none for the mediocre. And strange to say, Cæsalpino, though secluded from the botanical centers of Holland, France, and Germany, rose to hold the palm as the most brilliant of his contemporaries. In modern times he is still revered as the father of systematic botany. To these men Porta was not known, and presumably they were not known to him either. To describe the principal episodes in the life of Porta, the various phases of his character and labor, history has little to say, fame less.

He was born in Naples, in the year 1545, and he did succeed in gaining reputation as a noted naturalist, philosopher, physician and pharmacologist. His home was a favorite gathering place for men of learning; meetings were held, dubbed "Accademia dei Secreti," and themes were discussed delving into all the mysteries of nature, principally the chimerical secrets of magic. That Porta held an eminent place among his associates seems proven by the fact that they regarded him as "a new prophet," and as such Porta was summoned to the court of Rome to defend himself. He must have made a bold stand, for instead of meting out some punishment for his suspected, supernatural power, the court exonerated him and elected him a member of the Accademia dei Lincei. After that time he lived in Rome for several years, and he died in February 1615. The only botanical work written by Porta is "Phytognomonica," published in Naples, 1588. Three subsequent editions, 1591, 1608, and 1650, were published in Germany. In the later years of his life Porta acquired no small notoriety as an author of dramas and tragedies. Considering the profuse material treated in "Phytognomonica," and the fact that Porta was only in

his forty-fourth year when the work appeared in print, he must have begun his botanical career at a very early age.

In this work, "Phytognomonica," Porta introduced a new system for plants, but far different from those established by his contemporaries or predecessors. His mind, evilly influenced by the extravagancies of the Paracelsistes, dwelt mostly upon such singular phases, remote from natural history, as similarity between parts of plants and organs of man and animals, or the resemblance of parts of plants with diseases of man and animals, furthermore the habit or aspect of plants as being analogous to those of man, and finally the relation of plants to the stars, the sun, and the moon. Nevertheless Porta was a botanist, and a very learned one. His studies of plants reveal more than a superficial knowledge of their parts, and he must have known many. But from beginning to end the system, or better the method, proposed by him was too enigmatic to conform with the requirements of natural science, founded as it was on principles so contrary to nature as they possibly could be; and so the system never reached beyond being considered the product of "l'imagination brilliante mais déréglée."[1]

It is, indeed, difficult to understand how a man so intellectually gifted as Porta would ever waste his time and labor on such problems as to demonstrate the secret virtues of plants by merely observing the forms of their parts and the color of their flowers. Thus according to Porta certain species of *Orchis* with the roots palmate, and grasses with the spikes in fives (*Cynodon Dactylon*) would be a safe remedy for diseases in foot or hand, for gout, etc.; plants with heartshaped roots or fruits (*Valeriana, Persea*) for heart disease; plants with the flowers resembling eyes (*Aster, Sedum*) for eye diseases. Furthermore, plants with spotted stems (Araceæ) would on account of their likeness to snake-skin be useful as

[1] Compare Planchon, J. E., "Des limites de la concordance entre les formes, la structure, les affinités des plantes et leurs propriétés medicinales," Thèse, Montpellier, 1851.

antidote for snake bites, etc. Forty-two sections of this type are described by Porta, and some are fairly well illustrated. Much attention is given to citing and explaining descriptions and names of species known to and mentioned by the old authors, Pliny, Dioscorides, Columella, and others, and from this particular viewpoint the book is quite interesting and useful.

But even if the greater part of this book is devoted to considerations of the secret virtues of plants, some chapters and remarks, scattered here and there, reveal the indisputable talent of Porta as an observer of plant life. To do full justice to this part of his work let us briefly consider the status of botany in the sixteenth century. It was an era of classification or attempted classification; the plants were described and arranged in some way as an expression of their mutual relationship. By Bock (1560) they were divided into herbs, shrubs, and trees; by Clusius (1576) the system became enlarged so as to comprise bulbous plants, plants with the flower fragrant or inodorous, plants with milky juice, etc. The descriptions furnished by Clusius have always been regarded as most excellent, but he gave much more attention to the foliar structure than to the floral; in this point of view he was followed by Lobelius and Dodonæus. Caspar Bauhin (1550–1624) established a system covering twelve books, and he began with the grasses and grass-like plants, including *Iris, Acorus*, etc.; after these came the bulbous plants, then those with large, edible roots, etc.; the genera were not described, only the species with a number of synonyms. Bauhin was the earliest author to use binary names; but in describing the plants he did not consider the structure of the flower, nor the fruit. Finally Cæsalpino (1583) not only established a system principally based upon the organs of fructification, hitherto ignored, but he added a large number of new observations of great importance to the study of botany. The introduction to his work contains a discussion of theoretical botany in general. With regard to his classification of the plants, into arborescent and herbaceous, the

minor groups, characterized by the structure of fruit and seed, are not natural, except the sixth, which comprises the Umbelliferæ, the tenth, Boragineæ and Labiatæ, and the fifteenth, plants destitute of flowers and fruits, ferns, mosses, and fungi.

Naturally the tendency to classify governed botanical research during as early a period as the sixteenth century, and the various systems proposed were all purely artificial. Not until the year 1703 were the Phanerogams distinguished as mono- and dicotyledonous by Ray. We remember that so late as the middle of the eighteenth century Linné established his artificial system, based upon the floral structure, and at about the same time Antoine Laurent de Jussieu undertook the task to describe the families. In other words, Bauhin wrote the diagnoses of the species, Tournefort (about 1700) characterized the genera, Linné arranged the genera in groups, which he named only, and finally Jussieu established a natural system with family-diagnoses. But returning to the sixteenth century, the actual knowledge of the plants was embodied in systems, and beyond the mere classification no attempts were made to consider the plants from a biological viewpoint, as members of a living world adapted to environments of highly different nature as to climate and soil, at least not in accordance with the history of botany. The treatment of this particular phase of plant life was reserved to the very close of the nineteenth century, when Warming[2] introduced a supposed new branch of botanical science, dealing with plant societies, now universally recognized as plant ecology. The appearance of this work has brought about a fuller valuation of the factors that govern plant life, a purely biologic consideration of the plants on morphological and physiological grounds. However, twenty years of experience has taught us that this branch of botanical science lacks organization and is yet rather to be compared with a speculation having run far in advance of facts. Nevertheless the supposed new doctrine

[2] "Plantesamfund," Kjœbenhavn, 1895.

does exist, and has existed for more than three centuries, founded by Porta, and amply discussed in several chapters of his "Phytognomonica." No mention is made by Warming of Porta's book. And, strange to say, no mention is made of Planchon's either. By Sachs[3] Porta is passed by in silence.

Planchon (*l. c.*), Guy de la Brosse[4] and Adanson[5] refer only to the part dealing with the secret virtues of plants; the chapters on plant societies are ignored, or let us say not appreciated.

To Porta the method of classifying plants as instituted by his contemporaries must have been absolutely unknown; of rendering the knowledge of plants more accessible by means of a system he had no thought. His principal object was to demonstrate the virtues or properties possessed by plants, and, as stated above, Porta combined these with the general aspect of plants, the shape of their leaves, stems, etc. While making these observations in the field, as he did, Porta became aware of the distribution of a number of species under conditions very variable, and especially with regard to the soil. He noticed the fact that the general aspect of the plants, their shape, color, odor, hairiness or smoothness, at least to some extent, depended upon the environment in which they grew, and from this point of view, we might say "biologic," did Porta elaborate the introduction to his "Phytognomonica." He divided the plants in two groups, aquatic and terrestrial, each with several subdivisions. Of the former, examples are given of species characteristic of lakes, swamps, rivers, brackish marshes, etc., and he described the habit of several plants, in most cases very correctly. With respect to the terrestrial plants Porta distinguished between those that occupy a rich, a dry, or a sandy soil, illustrated by *Malva*, *Lithospermum*, and *Fœniculum*. Furthermore, some amphibious species are described, such as are terrestrial but

[3] "Geschichte der Botanik," München, 1875.

[4] "De la nature des plantes."

[5] "Familles des plantes," Vol. I, préf., p. ii, 1763.

adapted also to live in the water. In several chapters descriptions are given of the habits of plants, of species characteristic of the mountains, the lowlands, the hillsides, and the shady valleys; to these were added some brief remarks upon the vegetation of the northern, the temperate, and the torrid zones. Among the cultivated plants Porta mentions *Zea*, which, however, is not the plant known now under this name (maize), but a kind of wheat (*Triticum Spelta*) as demonstrated by De Candolle. In bringing these facts together Porta certainly laid the foundation of plant ecology, and the classification, proposed by Warming (*l. c.*), of the various plant societies: "*Hydrophytes, Xerophytes, Halophytes* and *Mesophytes*" is not much more instructive than the one introduced by Porta: "plantæ palustres, fluviatiles, marinæ, salsæ aquæ, silvestres," etc.

Naturally these groups have received a more elaborate treatment by authors of a recent date, especially with reference to the internal structure, which often, but very far from always, is in correlation with the respective environment. However, the weakness of modern ecology rests on the belief that the structures may be explained as caused by the natural surroundings. Experience has taught that the genera and species do possess some character of their own, which they never give up. To a certain limit the plants may allow themselves to submit to changes, but beyond that they will sooner die.

So far as Porta considered the biologic question of plant life, dealing only with the superficial aspect, more or less comparable to the surroundings, he committed no errors of consequence. For as a matter of fact the principal features exhibited by members of plant societies are mainly external, such as the shape of leaves, their relative size, the organs of vegetative reproduction, and the general habit; the internal structure cannot be relied upon, at least not at the present stage of our knowledge of plant life.

Thus already in the sixteenth century the first essay on plant ecology appeared, and Porta was the author.

SHORTER ARTICLES AND DISCUSSION

AN AUTOSOMAL BRISTLE MODIFIER, AFFECTING A SEX-LINKED CHARACTER

A RECESSIVE gene in the third chromosome of *Drosophila melanogaster* (*ampelophila*) affects the bristles on the thorax and scutellum of females which are heterozygous for a recessive sex-linked character, forked in such a way as to make forked semi-dominant. This latter character has been described by Morgan and Bridges (Carnegie Publ. 237). The bristles of "stock" forked flies are shortened, twisted, and heavier than normal. This applies to the bristles of the head, thorax and scutellum. Flies heterozygous for forked, that is, females, since the gene is in the X chromosome, have normal bristles unless the fly is also homozygous for the third chromosome modifier here recorded. Females with one forked gene and one normal allelomorph, which are homozygous for a modifying gene in the third chromosome, are intermediate in appearance between forked and normal flies, and are designated as "semiforked." The males never show the character since they are never heterozygous for sex-linked factors. The forked appearance is limited to a few of the thoracic and scutellar bristles and the bristles in general are less affected than are those of the homozygous forked flies as regards thickening of bristles and twisting. Both of the third chromosomes must bear the modifying gene in order to affect the bristles. In the absence of the forked gene, the semiforked genes, even when homozygous, are nearly always without effect, but occasionally a few individuals may be detected which have shorter and heavier bristles, but this is not pronounced and is rarely found. Flies which are known to be pure both for forked and for the modifier, semiforked, can not be distinguished from the simple forked individuals without the modifier.

ORIGIN OF SEMIFORKED

The semiforked character was first observed in February, 1918, in the heterozygous Bar forked daughters resulting from culture 668, a cross of a Bar male from stock to a forked female of a non-disjunction strain which had been used to observe non-

disjunction for about three months previous to this mating. The semiforked females were not noticed until the bottle was half through hatching, probably being overlooked. The counts show that after the new character was found there were 15 such females and 42 of the expected normal bristle type. This is clearly a 3 : 1 ratio and both parents must have been heterozygous for the semiforked gene. Although they were not brother and sister, this is not improbable, because the gene seems to have existed originally in the Bar stock, which, however, was not pure for it. The forked female doubtless obtained the gene from the Bar stock also, as her pedigree contains many Bar stock males used in the non-disjunction experiments. Since attention was paid only to the behavior of the X chromosomes, it is easy to see that the autosomes would be interchanged from generation to generation and the forked female could have a third chromosome which came originally from the Bar stock.

The strain was kept going by brother-sister matings. One F_2 culture (712) of a forked male to a heterozygous Bar forked female, which was semiforked, produced all the heterozygous forked females with semiforked bristles. Here both parents were pure for the modifier. In Culture 722, which was an F_2 from 668, half of the females heterozygous for forked were semiforked. In this case, one parent was pure and the other heterozygous for the modifier. One case was observed where a forked male crossed to a semiforked female produced no semiforked daughters. The explanation is that both the third chromosomes of the father carried the normal genes. The reverse case of this was shown when a forked male was crossed to a heterozygous Bar forked female with normal bristles. Of the heterozygous forked females produced, approximately half were semiforked and half normal bristled. Here the father was pure for the modifier but the mother was heterozygous for it and the 1 : 1 ratio resulted.

Location of Modifier

The presence of the modifying gene in the third chromosome was demonstrated by the following method, which has been used before in work on *Drosophila*. A semiforked female was outcrossed to a star dichæte male from stock. Forked star dichæte males were selected from the offspring and back-crossed to the semiforked females from stock cultures. Star and dichæte are dominants in the second and third chromosomes respectively

and are used because they can be easily detected in the heterozygous condition. Since there is no crossing over in the male in *melanogaster*, any dichæte fly in the offspring of the back-cross must have obtained one third chromosome from the dichæte stock and one from the semiforked stock. Any fly which was not dichæte traces back both its third chromosomes to the semiforked stock.

Examination of the offspring from the back-cross in three cultures showed that no dichæte fly was ever semiforked and, conversely, all not-dichæte females were semiforked, provided they were heterozygous for forked, and this includes all those not homozygous forked. About 500 individuals were obtained from these three cultures and the above statement is based upon them. The result is absolutely clear-cut and shows that the modifying factor is recessive and in the third chromosome. The presence of the star chromosome (II) did not affect the appearance of the semiforked character in any way. The location of the gene within the chromosome by its linkage relations to other third chromosome genes has not been carried out.

Summary

1. A recessive third chromosome modifying gene converts heterozygous forked females into intermediate semiforked individuals.

2. Homozygous forked flies are not visibly affected by the modifier.

3. The semiforked modifier rarely produces any visible effect when homozygous unless the forked gene is present.

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MIGRATION AS A FACTOR IN EVOLUTION: ITS ECOLOGICAL DYNAMICS[1]

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I. INTRODUCTION

MY subject, "Migration as a Factor in Evolution," is, in other words, the function or rôle of migration in evo-

[1] This paper was prepared, by invitation, for the symposium on the Factors of Evolution, at the Pittsburgh meeting of the American Society of Naturalists and an abstract of this paper, entitled "Migration as a Factor in Evolution," was read January 1, 1918. Dr. G. H. Shull, president of the society, has kindly consented to its publication in advance of the volume which is to contain all the papers of the symposium.

lution.[2] In view of the recent concentration of interest on heredity, my subject has the flavor of an old-fashioned one, which calls back to the days when Darwin and Wallace were living, and when Wallace's "Island Life" was frequently read with enthusiasm, and when there was possibly a more general belief that natural selection was one of the large factors in evolution. But progress has not been limited to the studies of heredity, for with the rapid rise of certain phases of general physiology, animal behavior and animal ecology, a newer orientation is now possible with regard to the migration of animals by both the active and passive methods. For our knowledge of animal responses, as well as the influence of the vegetational and physical environment, have made considerable progress, and we now probably see more clearly than ever before the intimate relation existing between the animals and the conditions which influence their migrations. The present occasion has thus furnished an opportunity to make a preliminary reorganization of the accumulated materials from a somewhat different standpoint than was formerly current in discussing migration. And although some of these ideas are widespread and even commonplace in certain limited fields, yet they are not yet in as general use as is desirable, and they are in urgent need of extended application and critical study.

In the following discussion of migration as an evolutionary factor, I wish to emphasize two points in particular. One is the discussion of the process of analysis and the other is to suggest some methods of applying this method to the problem of migration. It may seem aside from the main thesis to give this emphasis to the process method of evolution, but after striving several years for the conscious application of this method in an allied field (Adams '13, '15), and seeing its beneficial results there,

[2] By evolution, I mean to use the term in the broadest possible sense—to include all changes within the organism and its necessary environmental implications, and not as limited to the "species problem." This term must be as thoroughgoing as metabolism in physiology, or as metamorphism as applied to rocks by Van Hise, "any change in the constitution of any kind of rock."

and furthermore, not having seen this formulated and applied to evolution as here presented, I feel that the importance of the subject merits this treatment.

Special attention is called to the fact that this discussion is not intended as a complete, scientific explanation of migrational facts, but as the presentation of a point of view, or working hypothesis, which it is believed will aid in explaining many well-known facts and relations, and will aid in the discovery of new ones. An effort has been made to frame this hypothesis in such a manner as not to prejudice the problems investigated, or to interfere seriously with the various constructive schools of investigation, although I am well aware that this hypothesis, like all others, is built upon certain assumptions.

During the preparation of this paper (which amplifies certain ideas which I have previously outlined) I was much impressed by finding so much confirmatory evidence of the general validity of the dynamic standpoint, in fields relatively remote from migration. The independent growth of such conceptions in diverse fields is indicative that many subjects are independently reaching a certain common stage of development and that spontaneously such ideas are becoming independent organizing centers of activity. By interaction and regulation among these ideas, new higher systems of unity and correlation are developing, which are producing important effects in zoology as well as in other sciences. The slowness seen in the application of dynamic ideas to biology is perhaps rather natural as is evident when we recall the fact that even in the simpler physical sciences we have as yet no complete dynamical theory or system, although much progress has been made, not, however, toward a complete system, but toward that dynamic equilibrium which characterizes a growing subject.

II. The Process Method of Animal Responses

1. Introduction

The fundamental assumption upon which this discussion is founded is that the animal should be looked upon

as an entity or agent whose system of activity or responses to internal and external influences are its most fundamental characteristic. The activity of the animal, as an agent, is its *process* of change or its process of activity. Broadly speaking, this is a study of influences, of response or behavior, a study of what animals do and how they do it. Throughout it is the *dynamic* aspect of the animal; the pressure it exerts upon the environment; and the pressure exerted by the environment on it, that is of greatest importance. I see no reason why these assumptions can not be of universal application, and why they can not be accepted in all investigation. This view appears to be so well established that no detailed evidence and discussion of it seems necessary at this time. The animal agent itself is not a fixed thing, but one which runs through a cycle; it originates, develops and disintegrates and is thus in its maintenance subject to all the ebb and flow of other processes, and has similar dynamic relations. There is thus valid reason for assuming a thoroughgoing process or dynamic program for dealing with all animal problems. The same is equally true of all plants which form a part of the animal environment, and the physical environment lends itself, in fact, easily leads, in such a treatment, and fits into this scheme harmoniously, and makes it possible to give not only a uniform treatment to all phases of animal relations, but enables the student of animals to make a perfect contact with all the allied sciences, and to draw from each one all possible support, with the least possible friction and interference.

2. *Dynamic Principles*

(*a*) *Activity of Agent.*—In discussing animal problems from the process standpoint there are several conceptions which are fundamental. These ideas can be illustrated in simple form by an example from physical science. Running water is a substance combined with energy (gravitation) which exerts stress or pressure, which it expends upon other substances, and it is therefore an agent. An agent thus exerting stress and expend-

ing gravitational energy upon other substances is in the process of activity. Thus, running water, by the general process of erosion, including the subsidiary processes of weathering and transportation, wears down the land and results in the formation of many features such as brooks, creeks, plains, deltas, and a variety of other physiographic products. An organism is also an agent which expends physical and chemical energy, producing stress and exerting pressure and expending energy on other substances, exhibits its process of response or its *process of behavior.* An animal, by the process of predation runs down another animal and devours it, by its *process* of digestion dissolves it, and by the process of assimilation makes muscle, bone, feathers or fur out of it, and these are all products of its activity. The process of response is here strictly comparable to the process of erosion of running water, and their products are similarly comparable. The general process is generic and includes many species and varieties of subsidiary processes, *ad infinitum.* As Keyes ('98) has well said, "Processes are merely operative. If coupled with products at all . . . they must be regarded as formative or constructive. The product's destruction, its loss of identity, is wholly immaterial. The action of agencies is merely to produce constant change." It is, therefore, to the process of living, to the process of evolution, rather than to its products such as species, varieties, etc., which are of fundamental importance. For this reason the products must be subordinated to the agencies and processes, because the laws of change are in reality the object sought.

The physiographer is not content to rest with the idea that the agent, as, for example, running water, is the finished product of his analysis, for he also applies the same methods of investigation to the agent itself, in order to know its method of origin, the *process* by which it originates in the stream, whether indirectly from a spring, or directly from the clouds. Thus the same methods which the physiographer uses in studying the activity of the agent, he again uses to explain the origin or derivation

of the agent iself. The investigator of animals follows the same plan. He likewise uses the same kind of methods in the investigation of the processes of functional and structural development, not only as applied to the actions of the agent, but to its origin as well, and thus again we are justified in concluding that the process method is of universal application.

(*b*) *Cycle of Activity.*—The activity of agents is always accompanied by the expenditure of energy. This expenditure does not take place at a uniform rate, there is a pulsation, an ebb and flow, a rising and a falling. Periods of activity are followed by periods of repose and a rhythm is seen which can often be resolved into cycles. The importance of determining such cycles has been well expressed by Lockyer[3] as follows:

> Surely in meteorology, as in astronomy, the thing to hunt down is a cycle, and if that is not to be found in the temperate zone, then go to the frigid zones, or the torrid zones and look for it, and if found, then above all things, and in whatever manner, lay hold of, study it, record it, and see what it means. If there is no cycle, then despair for a time if you will, but yet plant firmly your science on a physical basis . . . and having gotten such a basis as this, wait for results.

There are innumerable cycles in the responses of animals, and of these the life-history cycle is perhaps the most generally recognized; but activity and response, hunger and satiety, stimulation and response, are other familiar expressions of these conditions. During these cycles of change the relative amount of energy set free varies greatly, in other words, its *dynamic status* changes. As expressed elsewhere, I have stated ('15, p. 10):

> When a great amount of energy is being set free, when an animal is exerting much influence, we may look upon it as producing pressure or strain. A condition of stress is not a permanent one, because the pressure tends to cause such changes as will equalize or relieve this condition. This is considered as the process of adjustment to strain, and is Bancroft's law ('11). An animal in an unfavorable condition is stimulated, its normal activities are interfered with, and a physiological condition of stress is produced which lasts until, by repeated responses or

[3] "Solar Physics," 1874, pp. 424–425.

"trials," the animal escapes stimulation or succumbs and a relative equilibrium is established. An area becomes overpopulated and consequently there may be established a condition of stress which results in an adjustment by a reduction (through many causes) in the excess of population and a restoration of the normal, or a condition of relative equilibrium. From these examples it may be seen that the *dynamic status* means the condition of a unit or system with regard to its degree of relative equilibrium. The cycle of change may be considered to begin at any point. I have taken as the initial stage of the cycle the condition of *stress* and *pressure* and have indicated how this condition tends to change in response to pressure, bringing about the *process* of adjustment to strain, and leading to the *condition* of adjustment to strain, or that of relative equilibrium. The activity of the agent produces the condition of stress, the process of adjustment to the strain follows, and this leads to the product—the establishment of the condition of adjustment or of relative equilibrium.

These ideas can be well applied to the life cycle, as is indicated from the following statement by Sedgwick ('10, p. 177), who says:

The life-cycle, of which the embryonic and larval periods are a part, consists of the orderly interaction between the organism and its environment. The action of environment produces certain morphological changes in its organism. These changes enable the organism to come into relation with new external forces, to move into what is practically a new environment, which in its turn produces further structural changes in the organism. These in turn enable, indeed necessitate, the organism to move again into a new environment, and so the process continues until the structural changes are of such a nature that the organism is unable to adapt itself to the environment in which it finds itself. The essential condition of success in this process is that the organism should always shift into the environment to which the new structure is suited—any failure in this leading to impairment of the organism. In most cases the shifting of the environment is a very gradual process (whether consisting in the very slight and gradual alteration in the relation of the embryo as a whole to the egg-shell or uterine wall, or in the relations of its parts to each other, or in the successive phases of adult life), and the morphological changes in connection with each step of it are but slight. But in some cases jumps are made such as we find in the phenomena known as hatching, birth, and metamorphosis. . . . And with this property of reacting to the environment goes the further property of undergoing a change which alters the relation of the organism to the old environment and places it in a new environment.

It is seldom indeed that one finds ontogeny so clearly expressed in terms of an active agent which is under-

going a cycle of changes—both in structure and function—and is being stimulated, responding, behaving, and even migrating into new environments, in response to internal and external stimulation. This is indicative of the dawn of a new era in the study of ontology (cf. Thompson, '17). As Bancroft ('11, p. 178) suggested, Sedgwick ('10, p. 177) saw clearly for the moment, as it were, but not in practice and concretely, the dynamic conception of individual development, although it is very evident that he saw the unity or continuity of the ontogenetic cycle. However, it has remained for Child ('15, '15*a*, '15*b*) who, apparently adapting largely the dynamic conceptions of the plant and animal ecologists, and to a lesser degree those of the physiologists, has now given expression, in a clear and concrete manner, to the dynamic ideas in individual developmental responses, and special attention is called to his important work.

That the life cycle varies in its degree of susceptibility to environmental influence has been pointed out by Vernon ('99, p. 199), DeVries (1900), Bancroft ('11, p. 175), and others (Woods, '10; Pike and Scott, '15; Pike, '17). Vernon's law is expressed ('03, p. 199) as follows: "In fact, it would seem to be a law of general application that *the permanent effect of environment on the growth of a developing organism diminishes rapidly and regularly from the time of impregnation onwards.*" Bancroft was the first to see that his law included Vernon's. He said ('11, p. 175):

> We know that, as we get older, our tendency to resist change increases; our habits of body and mind become more fixed.[4] We should therefore be tempted to conclude that the resistance to change increases as the organism becomes mature and that a given stimulus would probably have the most effect if applied at or before the earliest stages of development.

[4] In this connection it is interesting to recall the influence which this law may have upon scientific research. Once Clerk-Maxwell wrote to Herbert Spencer about some point in his "First Principles" as follows: "It is seldom that any man who tries to form a system can prevent the system from forming around him; and closing him in before he is forty. Hence the wisdom of putting in some ingredient to prevent crystallization and keep the system in a colloidal condition." (Footnote by C. C. A.)

He then quotes Vernon and continues:

If the pressure on a liquid is made less than the vapor pressure for that liquid at that temperature, some of the liquid vaporizes, the temperature falls, and the liquid may be said to adapt itself to the new conditions. What would happen if the liquid were not adaptable? The easiest way to obtain non-adaptable liquid is to place a Bunsen burner under it. The temperature rises until the boiling point is reached. The liquid then ceases to be adaptable. It volatilizes, it disappears, it becomes extinct so far as that particular region or flask is concerned. If a species can not adapt itself to changed climate or other conditions, it does not volatilize; but it disappears, it becomes extinct. It may be a new point of view to consider the extinction of the mastodon as analogous to the distillation of water; but the two cases are really parallel, except in time.

These facts are of the greatest importance because they indicate the *critical stage or condition* at which, in the migration of animals into new localities and conditions, organisms are most likely to be modified, and thus influence their evolution. This furnishes a new reason for stressing the importance of the breeding conditions and habitat in ecology.

An exception to Vernon's law is to be seen in the case of the Protozoans (and probably to other kinds of non-sexual reproduction), as is indicated by Jennings ('12, '13) and Woodruff's investigations, which show that in a proper environment the inertia of the life cycle tends to continue on indefinitely and does not run down. Jennings ('12, pp. 573–574) shows that conjugation in Protozoa and sexual reproduction in the metazoa cause diverse and new combinations of characters. In other words, this means that the processes of conjugation (favored by adverse conditions) and sexual reproduction, tends to break up the stability and crystallization into which the ontogenetic system tends to develop, and tends to restore, as it were, flexibility and a colloidal state to the race. This changes the system so as to minimize the interference with its processes. In the metazoan the number of systems is so large, that in spite of its chemical integration and regulation, interference with one or more of

them, possibly the "slowest," limits action and causes death. As indicated later, according to the phase rule the greater the number of "phases" interacting the lesser the number of possibilities of change. This is not a condition limited to organisms, but is a general law. It is perhaps in some sense as this that we can concede "differentiation" as a cause of death.

The animal as an agent, or individual, behaves according to its own system, to the extent that it is an independent unit, and these activities are cyclical. All systems tend to perpetuate themselves. Bancroft's law for all systems is that: "The broadest definition of it is that a system tends to change so as to minimize an external disturbance." In other words this is a perpetuating tendency, a method of assimilation, of which reproduction may be considered but a special phase; it is not solely a peculiarity of organisms, as is often stated, but of *all systems.* Sedgwick ('10, p. 177) has said: "It is a property of living matter to react in a remarkable way to external forces without undergoing destruction. . . . This property of reacting to the environment without undergoing destruction is, as has been stated, a fundamental property of organisms." In these features the animal acts only as other systems tend; as a catalyzer, it hastens changes and maintains itself. The activity of the animal, its centrifugal stress, causes it to collide with its environment, while, on the other hand, there is the environmental bombardment, both of which, within certain limits, tend to interfere or destroy the animal. On the other hand, the tendency of the system is to "minimize disturbance," to change within, to minimize, to "retreat" from interference (absolutely or relatively), and in this manner to a large degree, the system is perpetuated. To be sure, many individuals perish, but the system of the species continues. The rate of change of the system can be modified only as fast as its *slowest member* can change, and on this account many individual systems are destroyed.

In addition to influences which "interfere" with sys-

tems, as expressed by Bancroft, there are those which *reinforce* or accelerate (tend to continue or hasten activity) and do not change its character, but only the intensity of the response (temperature, enzymes, repetition, etc.). By this method also systems tend to be perpetuated, and organisms in "favorable" (non-interfering) conditions, tend to continue their normal activities.[5] This law appears to be a corollary of Bancroft's law which is concerned with interference or retardation. Thus when a system is *reinforced*, rather than disturbed, the system continues onward in its normal cycle without interference, and may even be accelerated in its activities. This is a condition which may maintain a relative equilibrium, or increase stress. The intensity of interference, or reinforcement, and its repetition, hastens or retards the rate of change of a system. We thus have the qualitative and quantitative relations applying to the law of reinforcement or acceleration of the equilibrium, and Bancroft's law of interference with its development.

Even relatively fixed and automatic responses of behavior may be looked upon much as the relatively stable structural characters, so that every sort of behavior, even to the process of higher learning, shows this regulatory influence which tends to change in such a manner as to eliminate all disturbance with its systems, even to the inconsistencies of our ideals.

Thorndike ('11, p. 244) in summarizing the laws of "acquired behavior or learning" formulates two laws. The first is essentially a statement of Bancroft's law of response to interference (discomfort or satisfaction), and the second (exercise or repetition), is that of reinforcement. This means that the kind and intensity of stimulation, and its repetition are the laws of establishing associations, or of changing the system, and that *intensity and repetition* act as the catalyzers which influence the speed of modification of the system; at bottom it therefore appears we have qualitative and a quantitative

[5] Cf. Jennings, '06, p. 295, "positive reactions."

expression of them. Limiting factors, because of their intensity and repetition, tend to change the animal system so as to minimize the external disturbance, or the animal system tends to change in such a manner as to minimize external disturbance, at a speed determined by the intensity and repetition of the disturbance. The so-called "trial and error," or, better, trial method of behavior, is also an independent formulation of Bancroft's law. It seems probable that the modifiability of behavior, and even *all methods of animal regulation, are expressions of these laws of interaction.*

The "balance of nature" is a culminating phase of the cycle of adjustment to strain. As expressed elsewhere, I have said (Adams, '15, p. 14): "When a balanced condition, or relative equilibrium, in nature is referred to, we must not assume that all balances are alike, for some are disturbed with little effort and others are exceedingly difficult to change. This distinction is an important one. Once the balance is disturbed, the process of readjustment begins. This is a phase in the balancing of a complex of forces. Just what stages this process will pass through will depend, to an important degree, upon the extent of the disturbance. Slight disturbances are taking place all the time and grade imperceptibly into the normal process of maintenance, as when a tree dies in the forest and its neighbors or suppressed trees expand and take possession of the vacancy thus formed. Disturbances of a greater degree, on the other hand, may only be adjusted by a long cumulative process. This change can progress no faster than the rate at which its slowest member can advance. Thus a forest association of animals may be destroyed by a fire so severe that all the litter and humus of the forest floor is burned. The animals which live in the moist humic layer as a habitat, such as many land snails, diplopods, and certain insects, can not maintain themselves upon a mineral soil, rock or clay. As such a forest area becomes reforested, these animals can only find the optimum conditions when the slow proc-

ess of humus formation reaches a certain degree of cumulative development. Under such circumstances this later stage must be preceded by antecedent processes, and the restoration of the balance is long delayed. Some adjustments take place so quickly that little can be learned of the stages through which they pass. There are, however, many slow processes which afford an abundance of time for study; in fact some are too slow to study during a life time. The processes which are moderately slow are often particularly illuminating because all stages are frequently so well preserved that comparison is a very useful method of study; the slowness of a process has a certain resolving power, as it were, recalling the influence of a prism upon a beam of white light, which reveals many characteristics obscure to direct vision. A study of the processes of adjustment among animals is a study of an important phase of the problem of maintenance. The continued process of response will, if circumstances permit, lead to a condition of relative adjustment, or balancing among all the factors in operation.'' The determination of the dynamic status and its application to cycles is seen to be a method or criterion which may be used for the determination of cycles of activity, and the repetition of these determinations will indicate the direction of movement of a process, and thus serve as a guide in the determination of its rate of change.

(*c*) *Limiting Factors.*—Animals live in a real world, they are dependent upon an environment and they can not be understood independently of it. They do not live, as it were, in a vacuum. As Brooks ('02, p. 485) has said: ''No physiologist who studies the waste and repair of living bodies, no naturalist who knows living beings in their homes, no embryologist who studies the influence of external conditions upon development, can, for an instant, admit that living beings are self-sufficient or self-sustaining, or that their being is in themselves; for the line we draw, for our study, between living beings and the external world is not one we find in nature, but one

that we make for our own purposes." We have seen that the essence of the animal is its activity. Its life is a continuous collision with the environment and a bombardment by the environment, with changes which tend to relieve the disturbances. This is particularly true of free-living animals, and is indirectly so, even of sedentary and sessile kinds. This radiating activity of the animal, and the direct convergent influence of the environment on the animal, is the basis for the friction and interaction which exists between the organism and the environment. There are, therefore, definite zones of influence and stimulation about the normal or attuned environment of the animal, and with departure from these conditions locally and geographically there are certain definite results (Adams, '04, p. 211):

> The new vital conditions are a cause of stimulation and with further departure (beyond a certain limit) it leads to increased stimulation or to unfavorable conditions. This results in retarded growth, development, and reproduction of the organism as a whole. Thus the end results of extreme departure from the optimum in either direction are similar.

(Adams, '15, pp. 8–9):

> Thus departure from the optimum toward an increase or a decrease, are departures from the most favorable, conditions toward less favorable conditions and hence toward limiting conditions. . . . In nature we look upon the optimum as that complex of habitat factors which is most favorable, and departure in any direction from this optimum intensity is in the direction of a less favorable degree of intensity, or into unfavorable conditions. From this standpoint *any unfavorable condition is a limiting factor* and may retard, hasten, or prevent vital and ecological activities.

(Adams, '13, p. 98):

> The similar results of extremes of high and low . . . temperatures, aridity, and the lack of oxygen may be cited as examples. Such effects have an important bearing upon the subject of physical and chemical *limiting factors* which influence individuals. [Cf. Shelford, '11, pp. 598–599.]

I would now modify my preceding quotations so as to definitely discard the old idea of the optimum,[6] in harmony

[6] This word has a general utility, but its technical value, like that of the "normal," both long considered peculiar to organic response, appears to be limited.

with the suggestions of Blackman and Smith ('11) who show that certain physiological processes are better explained as the "result of interacting limiting factors than by the conception of the optima." This principle is an extension of the law of the minimum and is formulated by them as follows (p. 411):

> The identification of the particular limiting factor in any definite case is carried out by applying experimentally the following general principles. *When the magnitude of a function is limited by one of a set of possible factors, increase of that factor, and of that one alone, will be found to bring about an increase of the magnitude of the function* . . . (p. 397). When several factors are possibly controlling a function, a small increase or decrease of the factor that is limiting, and of that factor only, will bring about an alternation of the magnitude of the functional activity.

Probably this formulation should be broader, and be made to include not only a single factor, but all unfavorable or limiting factors, as I have indicated above, and as both Livingston ('17, p. 8) and as Hooker ('17, p. 201) suggest.

Recent additional physiological evidence of the concentric zonation (gradation) of the limiting factors of temperature and humidity have been made by Pierce ('16). He accepts the older idea of the optimum and thus certain of his results on zonation harmonize with my statement of 1904. He shows that for the cotton boll weevil there is a vertical temperature gradient which influences the metabolism, growth and other activities, and that for a given temperature there is a corresponding horizontal humidity gradient which forms concentric zones of less favorable conditions. These extend from the optimum, through dormancy, on to death. It seems likely, however, that the idea of "interacting limiting factors" explains his facts better than that of the optimum.

The idea of limiting factors in experimental work is now building up a laboratory idea of environmental complexity, even under controlled conditions, which corresponds closely with what the field ecologists have called

an environmental complex. This is a healthy sign as it will greatly assist in the correlation of field and laboratory studies. Recently Livingston ('17, p. 8) has said:

> I wish now simply to emphasize the point that we can no longer speak of a single condition as being a cause of an observed effect. The next generation of physiologists will have to learn to handle more than a single variable and to deal with *complexes* of conditions.[7]

This recalls John Stuart Mill's statement that:

> It is seldom, if ever, between a consequent and a single antecedent that this invariable sequence subsists. It is usually between a consequent and the sum of several antecedents; the concurrence of all of them being requisite to produce, that is, to be certain of being followed by the consequent. In such cases it is very common to single out one only of the antecedents under the denomination of cause, calling the others merely Conditions. . . . The real cause is the whole of these antecedents; and we have, philosophically speaking, no right to give the name of cause to one of them, exclusively of the others. . . . All the conditions are equally indispensable to the production of the consequent; and the statement of the cause is incomplete unless in some shape or other we introduce them all.

When Hooker ('17, p. 201) states that, "It is necessary to get away from the custom of discussing causes, however difficult this may be. The idea of causation invariably indicates *incomplete analysis*," he does not express the full significance of Livingston's remark. We have not yet outgrown Mill's statement.

In addition to its application to the individual animal, Bancroft's law applies with equal force to the dynamic tendencies of plant and animal associations. The dominance of a climax society shows that (Adams, '08, p. 125):

> Such dominance, in general, implies extensive range, relative abundance, and ability to indefinitely succeed or perpetuate itself under given conditions. . . . The primary environmental conditions tend to encroach upon all others. The local conditions thus tend to become transformed in the direction of the dominant environment and to be appropriated by it. The associations . . . are thus given a definite dynamic trend. . . . Minor environments tend to become encroached upon by the dominant regional influences and ultimately to become extinct. The succession of socie-

[7] Cf. Blackman, '05, p. 293, on the limitations of control experiments. C. C. A.

ties of local habitats is a declining one, while that of the geographic or climax habitat is an increasing and ascending one. . . . That the dominant geographic conditions tend to override local influences seems very fairly established because diverse local original conditions are transformed into the climax or dominant type.

To students of human economics (for except ecologists we seem to have almost no students of general economics, including wild animals and plants) Bancroft's law should be a revelation. The interference or friction seen in economics (Conant, '08) should be included under Bancroft's law. That these laws apply to human social conditions as well can easily be tested by any one who will venture to "interfere" with any system of social machinery, whether it be of the family, fashion, church, state or a political party, for very soon the pressure or stress exerted by the "system" will make itself evident, by the processes of coercion, persuasion, ridicule, proselyting, threat, ostracism, or by a final crushing effort; for interference with a dominant system whether it is large or small has but one tendency. Years ago Bagehot ('73, p. 97) clearly recognized what appears to be essentially the laws mentioned above, and applied them with great skill to the development of political history, under the names of "persecution" and "imitation." Persecution corresponding to interference and imitation to acceleration. Hooker ('17, p. 208) not recognizing Bancroft's law, suggests what he calls the "principle of integration" to cover the interaction of the systems which he recognizes. He says: "These systems are invariably overcoming the effects of limiting factors."

(*d*) *Interaction of Systems.*—The next higher category, above the animal system, is the *interaction of the systems*, and their principles of complex action. To be sure, the animal system can not be divorced from its environment, so that several important features of this interrelation have already been discussed briefly. In dealing with the organism and the environment these two gross systems are perhaps the most clearly recognized in biology. The

environmental complexity is so great that it is bewildering to many, particularly to those who have not followed the most recent methods of dealing with the vegetation and gross physical environment. For convenience in handling, this complex may be broken up advantageously into smaller systems or units which are the agencies which influence animals. This plan provides for both their qualitative and quantitative relations, because the agents provide for the qualitative units, and their dynamic relations include their quantitative intensities.

In dealing with the interaction of systems relating to animals, one of the first points to consider is the classification of these systems, and the recognition of the sizes of the units. Many groupings are possible, such as the individual animal, its plant and animal associates, and the numerous factors of the physical environment. Further analytical systems of the vegetational environment can be grouped according to the recognized units current among the students of the genetic aspects of vegetational development (see Cowles, Clements, etc.). For the physical environment the geologists, physiographers and geographers have already made much progress in the analysis of unit systems, which can be used with comparative ease (see Chamberlin, Salisbury, Van Hise, Davis ('09), etc.). In the study of all these systems naturally more progress has been made in their recognition, than in their complex modes of interaction; and the formulation of their laws of interaction is of the greatest importance. There are three models which really come to mind in this connection. These are:

1. The physical model of the interaction of forces, which leads to resultant motion.

2. The application of Bancroft's law to the interaction of all systems.

3. The application of the physical and chemical model of the phase rule of Gibbs to equilibria of all kinds.

These will now be considered in their respective order:

1. The physical model will assist in keeping in mind

the underlying relations that the stresses, exerted by agents, will reinforce, overcome or balance one another, and influence the end result of change. This is a quantitative law. The *inertia* of the process of adjustment, and the *inertia* of equilibria, should be recalled (cf. Newton's first law) in this connection. The conception of inertia appears to have been almost neglected in biology.

2. Bancroft's law, that systems tend to change to minimize external disturbance, is a general law which appears to apply to the *interaction of all systems.* This is a qualitative law, which should be of great practical value.

3. The phase rule, according to Henderson ('13, pp. 257–258) is that the

condition of equilibrium in any material system depends upon the number of its components, the number of its phases, temperature, pressure, and in general, the concentrations of all the components . . . [as to] the term "component" and "phase" it will here suffice to say that in general the number of components increases as the number of separate chemical individuals increases, and that a phase is any solid, liquid or gaseous part of the whole system which possesses homogeneity of composition. For instance, if a system is made up of sand, salt solution, ice and aqueous vapor, each of these separate parts in that it is homogenous, is a phase. . . . Other things being equal, the greater number of phases, the less the tendency to change.

The quantitative character of this rule makes its application one of great difficulty, but it will serve as a guide or model for the organization of problems, and suggests the form into which experimental data should be organized, and secured for testing its application and validity.

The following extracts from Findlay ('04, pp. 8–18) will assist in gaining some of the general ideas involved in this subject:

A heterogenous system is made up of different portions, each in itself homogeneous, but marked off in space and separated from the other portions by bounding surfaces. These homogeneous, physically distinct and mechanically separable portions are called *phases.* Thus ice, water, and vapor, are three phases of the same chemical substance—water. A phase, however, whilst it must be physically and chemically homogeneous, need not necessarily be chemically simple. . . . The *number of phases* which can exist side by side may vary greatly in different systems. In

all cases, however, there can be but one gas or vapor phase on account of the fact that all gases are miscible with one another in all proportions. In the case of liquid and solid phases the number is indefinite, since the above property does not apply to them. . . . It is important to bear in mind that equilibrium is *independent of the amounts* of the phases present.

By component (p. 10) is

meant only those constituents, the concentration of which can undergo *independent* variation in the different phases, and it is only with these that we are concerned here. . . . The Phase Rule is concerned merely with those constituents which take part in the state of real equilibrium; for it is only to the final state, not to the processes by which that state is reached, that the Phase Rule applies. (Pp. 11–13.) It is, however, only in the case of systems of more than one component that any difficulty will be found; for only in this case will a choice of components be possible. . . . Now, although these constituents take part in the equilibrium, they are not all to be regarded as components, for they are not mutually independent. . . . In deciding the number of components in any given system, not only must the constituents chosen be capable of independent variation, but a further restriction is imposed, and we obtain the following rule: *As the components of a system there are to be chosen the* SMALLEST NUMBER *of independently variable constituents by means of which the composition of each phase participating in the state of equilibrium can be expressed in the form of a chemical equation.* . . . Another method may be given by which the number of components present in a system can be determined. Suppose a system consisting of several phases in equilibrium, and the composition of each phase determined by analysis. If each phase present, regarded as a whole, has the same composition, the system contains only one component, or is of the first order. If two phases must be mixed in suitable quantities in order that the composition of a third phase may be obtained, the system is one of two components or of the second order; and if three phases are necessary to give the composition of a fourth coexisting phase, the system is one of three components, or of the third order. . . . Again, therefore, we see that, although the number of the components of a system is definite, a certain amount of liberty is allowed in the choice of the substances; and we also see that the choice will be influenced by the conditions of experiment.

Summing up, now, we may say:

1. The components are to be chosen from among the constituents which are present when the system is in a state of true equilibrium, and which take part in that equilibrium.

2. As components are to be chosen the *smallest number* of such constituents necessary to express the composition of each phase partici-

pating in the equilibrium, zero and negative quantities of the components being permissible.

3. In any given system the *number* of the components is definite, but may alter with alteration of the conditions of experiment. A certain freedom of choice, however, is allowed in the (qualitative, not quantitative) selection of the components, the choice being influenced by considerations of simplicity, suitability or generality of application.

We see, therefore, that in case of some systems two, in other cases, only one of the independent variables (temperature, pressure, concentration) can be altered without destroying the nature of the system; while in other systems, again, these variables have all fixed and definite values. We shall therefore define the number of degrees of freedom of a system as the *number of the variable factors, temperature, pressure, and concentration of the components, which must be arbitrarily fixed in order that the condition of the system may be perfectly defined.*

A knowledge of its variability is, therefore, of essential importance in studying the condition and behavior of a system, and it is the great merit of the Phase Rule that *the state of a system is defined entirely by the relation existing between the number of components and the phases present,* no account being taken of the molecular complexity of the participating substances, nor any assumption made with regard to the constitution of matter. It is, further, as we see, quite immaterial whether we are dealing with "physical" or "chemical" equilibrium; in principle, indeed, no distinction need be drawn between the two classes, although it is nevertheless often convenient to make use of the terms, in spite of a certain amount of indefiniteness which attaches to them—an indefiniteness, indeed, which attaches equally to the terms "physical" and "chemical" process.

The Phase Rule of Gibbs, now, which defines the condition of equilibrium by the relation between the number of coexisting phases and the components, may be stated as follows: A system consisting of n components can exist in $n+2$ phases only when the temperature, pressure, and concentration have fixed and definite values; if there are n components in $n+1$ phases, equilibrium can exist while one of the factors varies, and if there are only n phases, two of the varying factors may be arbitrarily fixed. This rule, the application of which, it is hoped, will become clear in the sequel, may be very concisely and conveniently summarized in the form of the equation—

$$P+F=C+2, \text{ or } F=C+2-P$$

where P denotes the number of the phases, F the degrees of freedom, and C the number of components. From the second form of the equation it can be readily seen that the greater the number of the phases, the fewer are the degrees of freedom. With increase in the number of phases, therefore, the condition of the system becomes more and more defined, or less and less variable. . . .

Systems which are apparently quite different in character may behave in a very similar manner. Thus it was stated that the laws which govern the equilibrium between water and its vapor are quite analogous to those which are obeyed by the dissociation of calcium carbonate into carbon dioxide and calcium oxide; in each case a certain temperature is associated with a definite pressure, no matter what the relative or absolute amounts of the respective substances are. And other examples were given of systems which were apparently similar in character, but which nevertheless behaved in a different manner. The relations between the various systems, however, became perfectly clear and intelligible in the light of the Phase Rule. In the case first mentioned, that of water in equilibrium with its vapor, we have one component—water—present in two phases, *i. e.*, in two physically distinct forms, viz., liquid and vapor. According to the Phase Rule, therefore, since $C = 1$, and $P = 2$, the degree of freedom F is equal to $1 + 2 - 2 = 1$; the system possesses one degree of freedom, as has already been stated. But in the case of the second system mentioned above there are two components, viz., calcium oxide and carbon dioxide, and three phases, viz., two solid phases, CaO and $CaCO_3$, and the gaseous phase, CO_2. The number of degrees of freedom of the system, therefore, is $2 + 2 - 3 = 1$; this system, therefore, also possesses one degree of freedom. We can now understand why these two systems behave in a similar manner; both are univariant, or possess only one degree of freedom. We shall therefore expect a similar behavior in the case of all univariant systems, no matter how dissimilar the systems may otherwise appear. Similarly, all bivariant systems will exhibit analogous behavior; and generally, systems possessing the same degree of freedom will show a like behavior. In accordance with the Phase Rule, therefore, we may classify the different systems which may be found into invariant, univariant, bivariant, multivariant, according to the relation which obtains between the number of the components and the number of the coexisting phases; and we shall expect that in each case the members of any particular group will exhibit a uniform behavior. By this means we are enabled to obtain an insight into the general behavior of any system, so soon as we have determined the number of the components and the number of the coexisting phases.

In the preceding quotations there are certain points to which special attention should be called:

1. The phase rule is concerned with equilibria, and not with the processes by which this state is reached. It thus supplements Bancroft's law in a very important manner, because that law is mainly concerned with the process of developing equilibria. To make complete continuity and

contact between these two methods and to fuse them into *one cycle* Bancroft's should also be quantitatively expressed (the interacting systems). The importance of this is evident. I have not seen attention called to this fact, or the intimate relation between these two laws.

2. The number of components, phases, independent variables, concentrations, etc., to which the phase rule applies, is also one of the most marked features of biological problems in its dealing with the relation of animals to diverse environmental conditions and media.

3. The analysis of biological problems into cycles of action, systems, and agencies, is a necessary simplification of the biological problems, and is preliminary to the determination of the number of components, phases, and concentrations which are involved in the application of the phase rule to equilibria, and to Bancroft's law of their development. Even in case of biological problems which have not been reduced to quantity this model of dynamic relations should be of much assistance in clarifying working plans, especially in associational studies.

4. Improvements in the dynamic theory will probably simplify its application to biology. The detailed non-mathematical expression of these correlations will facilitate their wider use in biology, and it is also equally evident that with an adequate mathematical equipment the biologist's application of these ideas would be greatly facilitated.

The phase rule has been so valuable chemically that a special effort should be made to use it as much as possible as a model in biological work. Mellor ('04, pp. 183–184) says: "Gibbs' phase rule is the best system extant for the classification of equilibria—chemical and physical. All changes, both physical changes of state and changes of chemical composition, are found to depend upon the same general laws." Henderson ('13, p. 260) remarks: "There can be no doubt that, when feasible, the ideal method—from the physico-chemical point of view—to de-

scribe a material system is in terms of the phase rule."[8]

To apply these principles to the interaction of systems is the great practical problem. It requires, as previously mentioned, the analysis of the problem to such a degree as to distinguish its different systems and homogeneous units, their degrees of freedom, their directions of change, their cycles, their dynamic status and their quantitative relations. Many of these action systems have long been clearly recognized by plant and animal physiologists and ecologists, as cells, tissues, organs and communities, and many are recognized also in the physical and chemical world, where much attention is given to dynamic relations.

The processes of integration and dominance tend to limit this diversity of systems. It is believed, however, that to strive consciously for the application of these conceptions with some idea of what they imply, will, however, greatly hasten progress. Further, by calling attention to these general ideas it may enable some investigators to become better prepared for handling them, because we may well recall Pasteur's remark that: "In the fields of observation chance favors only the mind which is prepared." It is hoped that by emphasizing these relations others better qualified than I am will give attention to this subject, and supply numerous examples in the various specialties; for it is by this method largely that others can become interested and extend the applications.

Up to this point the discussion has been mainly devoted to the development of a dynamic conception of systems and their methods of interaction. The migration of animals has long been recognized to include not only those caused by the activities of the animal itself, but also by the activity or agency of their environment; it is there-

[8] Henderson ('13) does not mention Bancroft's law or attempt to relate it to the phase rule. In my "Guide" ('13, p. 85) special attention was called to both Bancroft's law and the phase rule by listing these first among papers on dynamics. Recently, since this paper was written, I have seen Henderson's ('17, p. 138) criticism of Spencer's "stability of the homogeneous," to which he applies the phase rule and refers also to Bancroft's law, although not as here advocated.

fore now necessary to review briefly some of the main environmental agencies and processes operative. The geologists and physiographers have made much progress in the dynamic interpretation of their problems, so that it is a relatively simple matter to adapt their results to our purpose. They have shown that the rocks below the ocean are heavier than those of the land and that the present shores of the oceans change as a dynamic equilibrium is established between the heavier sea bottom and the lighter land area (Willis, '11). We have in this a cause for innumerable changes in the physical features of the earth's surface, and in the environments of animals. This beautifully illustrates the fundamental unity and method of interaction between the liquid sea and the solid land systems. This is one of the huge physical cycles which illustrate every dynamic phase, from a condition of stress through the slow process of adjustment to strain —retarded by the rigidity of the earth's crust—on to a dynamic equilibrium. All the land area which remains above sea level is exposed to waves, the disintegrating influences of the atmosphere, and the erosion by wind and running water, all of which tend to cut down all land to sea level, and to deposit the heavy débris on the sea bottom, thus cumulatively destroying its relative equilibrium, and, supplemented by radio-activity, there are instituted cycles of stress, in an unending series.

In the equilibria existing between the land and the sea, the isotatic cycle, and the cycle of erosion or base-leveling, are found two phases of the most important gross influences in the physical causes of animal migration (cf. Woodworth, '94; Adams, '01). To this must be specifically included climatic cycles (Huntington, '14, and others) whose influence upon animal migration is also profound. Intimately related to the preceding physical factors are the cyclic changes in the vegetational covering of the earth, particularly those recognized in recent years by the plant ecologists (Cowles, '11; Clements, '16, and others). The physical changes influence all organisms,

and operate in both short and long cycles, the various cycles traveling at diverse rates and mutually influencing one another in their adjustments to pressure. In these wonderful moving systems of cycles can be visualized the essence of modern scientific conceptions. From electrons, atoms, molecules, chemical compounds, colloids, cells, tissues, organs, individuals, and culminating in the community and association, is seen in each a dynamic center or microcosm, about which revolves other systems, in turn revolving as a part of a larger system in ever widening expansion, each in turn subordinated to a higher order of dominance, the culmination of interacting systems.

I have now completed an outline of the fundamental dynamic principles which are necessary as a background for my discussion of animal migration. These general principles appear to underlie all processes of animal regulation internal and external, and are expressions of these laws of interacting systems.[9]

[9] Although the preceding discussion is intended to bear mainly on migration, it should not be inferred that I would limit it in this manner. It is my belief that these general principles are of relatively wide application.

(*To be continued*)

A STUDY OF HYBRIDS IN EGYPTIAN COTTON

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INTRODUCTION

THE Egyptian type of cotton comprises numerous varieties which have presumably originated by mutation (Kearney, 1914). This presumption is based upon the following facts:

1. Each variety descended from a single individual which differed in several characters from the parent form.
2. The absence or extreme rarity of connecting forms and the infrequency of sterility in both the parental and the mutant stock make it difficult to account for these mutants on the basis of recombination, as ordinarily understood.
3. The new characters of the mutant are uniformly expressed in the successive generations of its offspring as long as hybridization with other forms is excluded.

The observed facts make it difficult to escape the conclusion that these mutants are the result of simultaneous alteration of several factors in the egg cell after fertilization.[1] Otherwise, it is necessary to assume that the mutant has resulted from the union of a male and a female gamete, in both of which similar but independent alteration had taken place with respect to several factors. Probability is so greatly against this interpretation as to make it almost unthinkable.

The question suggests itself, what are the conditions under which mutation occurs in Egyptian cotton? The appearance of mutants has thus far been observed only in mixed stocks (Kearney, 1918, pp. 60–61). Hence, not-

[1] A case of mutation has been thus explained by Hayes and Beinhart (1914).

withstanding the difficulty of interpreting the mutants as direct recombinations, the inference can scarcely be avoided that mutation in this group is conditioned by heterozygosity.

In an endeavor to obtain more definite information on this point it was decided to make simple and back-crossed hybrids between two varieties of Egyptian cotton and to study these hybrids in comparison with line-bred progenies of the parent varieties. Mutants in this group are of comparatively rare occurrence, nothing analogous to the "mass mutation" observed by Bartlett (1915) in *Œnothera* and by De Vries (1918) in *Zea* having been observed. Very large numbers of plants of the hybrid and parental stocks will therefore need to be examined before we may hope to obtain reliable statistics as to the production of mutants. In the meantime, it is believed that what has been learned in regard to the behavior of these hybrids in the first three generations is of sufficient interest to warrant preliminary publication.

Most previous studies of hybrids in the genus *Gossypium* have been made upon interspecific crosses, such as Sea Island cotton (*G. barbadense*) × Upland cotton (*G. hirsutum*) and Egyptian cotton[2] × Upland cotton. In these cases there is very great variability in the F_2 and later generations. Cotton breeders have found it to be practically impossible to "fix" such hybrids, even after selection continued during six or seven generations. On the other hand, little is known of the behavior of crosses between varieties within the same species. Are such hybrids less variable and less difficult to fix by selection, and, if so, can not stable and uniform new varieties be obtained by recombination? It is believed that these questions are partly answered by the data presented in this paper.

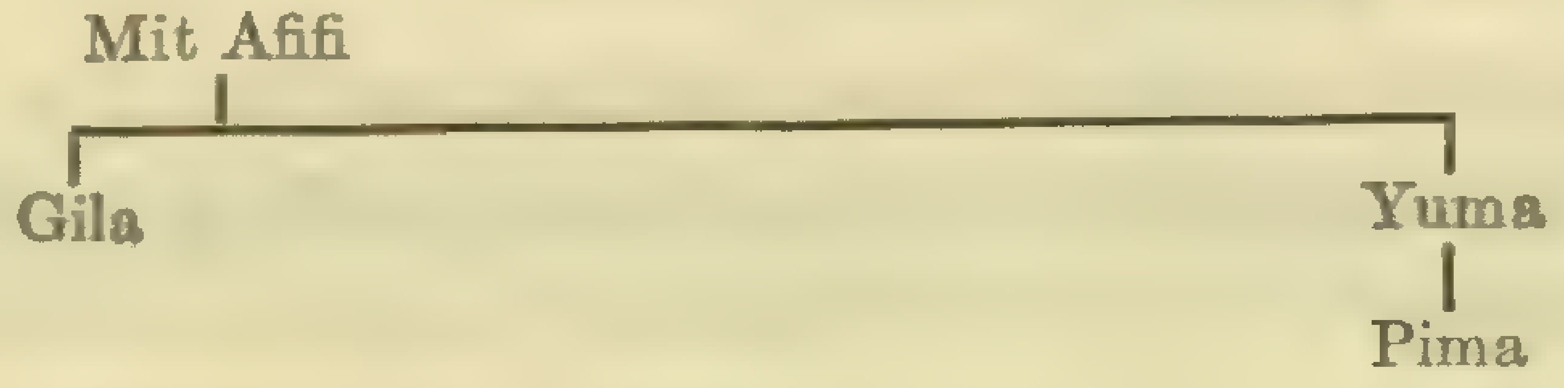
The investigation was conducted at the Cooperative Testing Garden, Sacaton, Arizona, which is conducted

[2] The Egyptian type of cotton, although commonly supposed to be of hybrid origin (Balls, 1912, pp. 3, 4) presents many analogies to a natural species and its differences from American Upland cotton are certainly of specific magnitude.

by the Bureau of Plant Industry in cooperation with the Indian Service. The writers are indebted to Mr. G. N. Collins of the Bureau of Plant Industry for many helpful suggestions throughout the course of the investigation.[3]

Plan of the Investigation

The only varieties of Egyptian cotton of which approximately pure strains were available when the experiment was begun were the Yuma, Gila and Pima varieties, all of which had been developed in Arizona. These varieties were described (with illustrations of the leaves, bracts, and bolls) and an account of their origin was given in an earlier publication (Kearney, 1914). Their relationship may be indicated thus:



The Gila and Pima varieties were chosen because they show the greatest amount of difference in the largest number of characters. Of the three varieties, Gila is most similar to the common ancestor, Mit Afifi, and Pima is the most distinct from it. Gila may, in fact, be regarded as representing a small portion of the area of variation of the extremely heterozygous Mit Afifi stock from which all these varieties have descended, while the characters of Pima are far outside the hitherto observed range of variation in Mit Afifi. The hybrids described in this paper may therefore be taken to represent, in a measure, the result of crossing the mutant Pima with its more remote ancestor, Mit Afifi.

Several typical individuals of each variety were selected in July, 1914. A number of flowers were self-pollinated on each plant and intervarietal cross-pollinations were made among them. The resulting first gen-

[3] It is not practicable to publish in full the voluminous data resulting from this investigation but the writers are prepared to supply, to any one who may be interested, photographic copies of the original records, at the cost of reproduction.

eration parental and hybrid progenies were grown in 1915. Seeds produced by flowers which were selfed on certain individuals in these progenies furnished the second generation, which was grown in 1916. Flowers on selected plants in the second generation parental and F_2 hybrid progenies were again selfed to furnish the third generation parental and the F_3 hybrid progenies, which were grown in 1917.

Some of the flowers on F_1 hybrid plants in 1915 were pollinated from plants in the first generation progenies of the original parent plants of either variety. From the resulting seed ¾ Pima and ¾ Gila back-crosses were grown in 1916. Plants were selected in each of the ¾ back-cross progenies because of their approach to the corresponding predominant parent in respect to important characters. The Pima back-cross plants were pollinated from a plant in the second selfed generation of the Pima parent and the Gila back-cross plants were pollinated from a similar Gila individual. The resulting ⅞ Pima and ⅞ Gila back-cross progenies were grown in 1917.

Every effort was made to grow the various parental and hybrid progenies under as nearly as possible uniform conditions in respect to soil, irrigation and cultural treatment. All comparisons of hybrids and parents have been made on the basis of progenies grown the same season, in order to obviate the influence of different weather conditions. Measurements on the different plants were made, as far as practicable, upon organs which occurred at the same nodes of the axis and branches and which were in the same stage of development. The number of plants on which most of the characters were measured in each generation were, in round numbers:

	F_1 (1915)	F_2 (1916)	F_3 (1917)
Pima	60	200	180
Gila	40	200	100
Pima × Gila	80	400	300

Characters Measured and Significance of the Varietal Differences

The Pima and Gila varieties, as represented by the first and second generation progenies of the selected parent individuals, differed by an amount equal to three or more times the probable error of the difference, in respect to 24 characters. Many of these are physically or physiologically correlated, but six of the characters showed practically no correlation inter se, in either parent. Most of these characters are expressions of size (*e. g.*, the length of the internodes, leaves, floral parts, bolls and fiber) or are ratios between two size characters and expressive of shape. The leaf index $\frac{\text{length}}{\text{width}} \times 100$ and the boll index $\frac{\text{length}}{\text{diameter}} \times 100$ showed especially significant differences between the two varieties named, the difference in the second generation having been 26 times the probable error in respect to leaf index and 46 times the probable error in respect to boll index. In length of fiber the difference between the parents in the second generation was 22 times its probable error. The only characters of diagnostic value which could not be accurately measured and which were therefore determined by grading, were color of the fiber,[4] amount of fuzz on the seeds and roughness of the boll surface (depending upon the depth, number and regularity of distribution of the pits in which the oil glands are situated). Even in respect to these characters the differences were of degree rather than of kind.

The Gila variety, as represented by three successive selfed generations of the progenies of the parent plants, gave larger coefficients of variation for most of the characters than did the Pima variety. Since no general decrease in the variability of either variety was observed after three generations of selfing, it would appear that Gila is inherently more variable than Pima.

The two varieties, as represented by the first and sec-

[4] The two varieties showed no difference in the color of any part of the flower.

ond generation progenies of the plants selected as parents of the hybrids, showed overlapping ranges for all characters excepting fuzziness of the seed and color of the fiber. These two characters were measured on only small numbers and overlapping would very likely have been observed if larger populations had been compared.

THE SIMPLE HYBRIDS

Means

Comparing the means of the simple hybrids (Pima × Gila) with those of the parents, a strong tendency to intermediacy was apparent. The means for a large majority of the characters, in both the F_1 and F_2, lay between the parental means, and in nearly one half of the total number of characters the hybrid means did not differ significantly from the midpoint of the parental means. The relative number of characters for which the departure of the hybrid mean was towards the Pima mean was much greater in the F_1 than in the F_2. This was probably due to increased vigor in the conjugate generation, eight of the thirteen characters which showed a significant[5] departure of the hybrid F_1 mean from the midpoint of the parents being size characters for which the Pima parent gave a larger mean than the Gila parent.

Eleven F_3 progenies of the simple hybrid were grown in 1917 from plants which were selected in the F_2 in 1916 because of their approach to one or the other parent or because of their intermediacy with respect to various characters, especially leaf index and boll index. The F_3 means for these characters in all cases fell between the means of the third generation parental progenies, or else did not differ significantly from the mean of one or the other parent.

Coefficients of Variation

In all three generations the hybrids gave significantly larger coefficients of variation, for most of the characters,

[5] A difference or other quantity is here referred to as "significant" when amounting to three or more times its probable error.

than did the corresponding selfed parental progenies of the Pima variety, but were not significantly more variable than the corresponding Gila progenies. In length of fiber the hybrid F_2 was not significantly more variable than either parent. The hybrid F_2 was significantly more variable than the F_1 in the leaf characters, but not in the boll characters. This result was so surprising that it was accepted only after repeatedly checking the original data. The averages of the coefficients of variation, for leaf index and boll index, of the eleven F_3 hybrid progenies did not differ significantly from the coefficients of the F_2 progeny from which they were derived. The average variability of the F_3 did not exceed that of the third selfed generation of the more variable parent (Gila) and two of the F_3 progenies were not more variable than the corresponding generation of the less variable parent (Pima).

These facts point to the possibility of obtaining a relatively uniform new variety of cotton by hybridization of two varieties belonging to the same general type, although hybrids between different types, such as Egyptian and Upland, are notoriously difficult to fix.[6]

Distributions

The distributions, for the important characters leaf index, boll index and fiber length, of the parental and simple hybrid progenies, are shown in Figs. 1 to 3.

The range of the hybrid F_2 for none of the characters appreciably exceeded the combined parental ranges and for the majority of characters it was more restricted than the latter. The variation was therefore much smaller than in the F_2 of hybrids between less closely related types of cotton, in which the range often greatly exceeds that of both parents. (For example, the Egyp-

[6] Longfield Smith (1915, p. 30) states that hybrids between the not very dissimilar Sea Island and Sakellaridis cottons were ''fairly uniform'' in the F_2 and F_3. Different behavior was shown by the cross between Sea Island and ''St. Croix Native,'' a type more nearly resembling American Upland cotton. In this case, ''new characters, not present in either of the original plants, appear in the first and subsequent generations,'' and the F_2 and F_3 ''split into a mass of types.''

tian × Kekchi hybrids described by Cook (1909, p. 12–14) and the Egyptian × Hindi hybrids described by Marshall (1915).)

Little or no evidence of dominance was shown by the distributions, for the various characters, of the F_1 of the

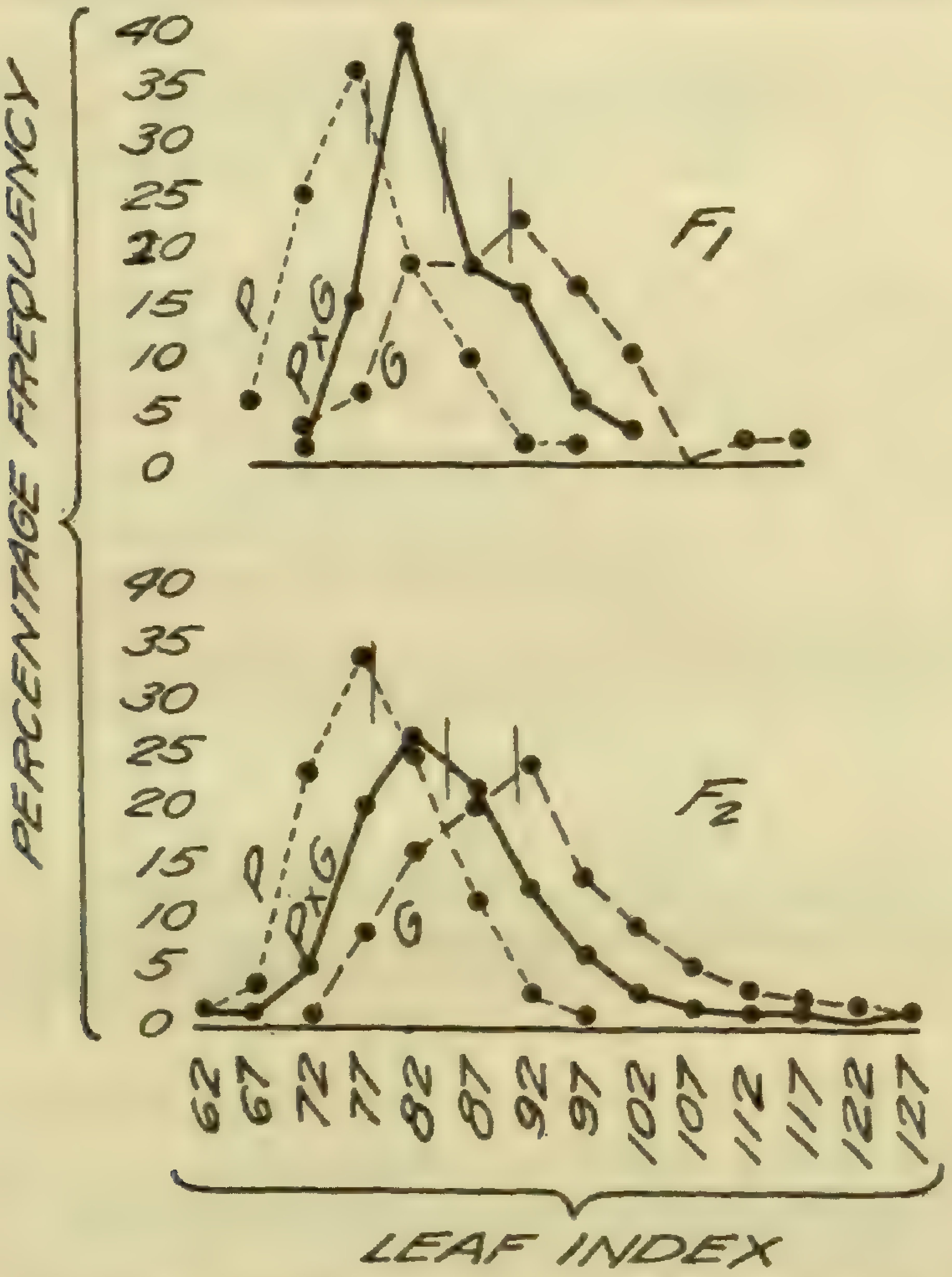


FIG. 1. **Leaf index: first and second generation distributions of the parental and simple hybrid progenies.** The dotted line curve represents the distribution of the Pima parent, the broken line curve that of the Gila parent and the solid line curve that of the hybrid. The short vertical line on each curve indicates the location of the mean of that population. The figures on the axis of ordinates indicate the number of plants in each class, taken as a percentage of the total number of the population. The figures on the axis of abscissas indicate the classes.

The actual numbers of the respective populations were: F_1, Pima 60, Gila 40, P × G 80; F_2, Pima 213, Gila 203, P × G 418.

simple hybrids. The F_2 distributions were strictly unimodal for all characters excepting the highly variable one length of axis, and even in this case the indication of bimodality was so slight as to be probably insignificant.

No evidence of segregation in definite ratios was obtained.

It is well known that complete dominance in the F_1 and 3:1 segregation in the F_2 are exceptional in size and shape characters such as chiefly distinguished the Pima and Gila varieties of cotton. On the other hand, the question whether the behavior of the Pima × Gila hy-

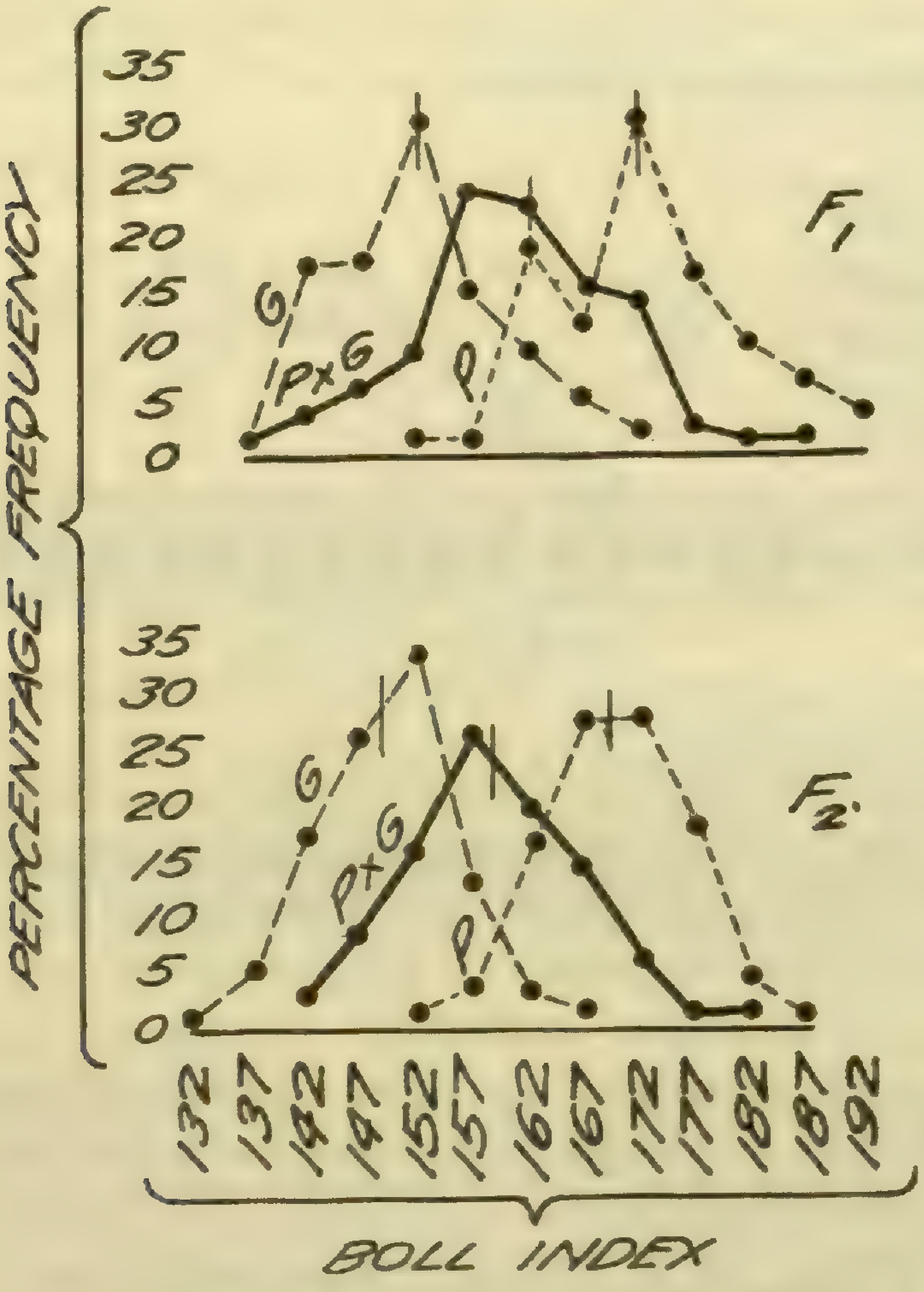


Fig. 2. Boll index: first and second generation distributions of the parental and simple hybrid progenies. Details as in Fig. 1. The actual numbers of the respective populations were: F_1, Pima 60, Gila 40, P × G 80; F_2, Pima 161, Gila 207, P × G 419.

brids with respect to such characters might be interpreted by the multiple factor hypothesis is extremely difficult to answer. The differences between the means of the parents for most of the characters, while small, are highly significant, but the parental ranges, in most cases, overlap to such an extent that Mendelian analysis would seem to be out of the question.

A few of the characters in respect to which these varieties differ significantly might be termed "qualitative." These are roughness of the boll surface, color of the fiber and fuzziness of the seed, all of which are included in the lists of allelomorphic pairs of characters in cotton

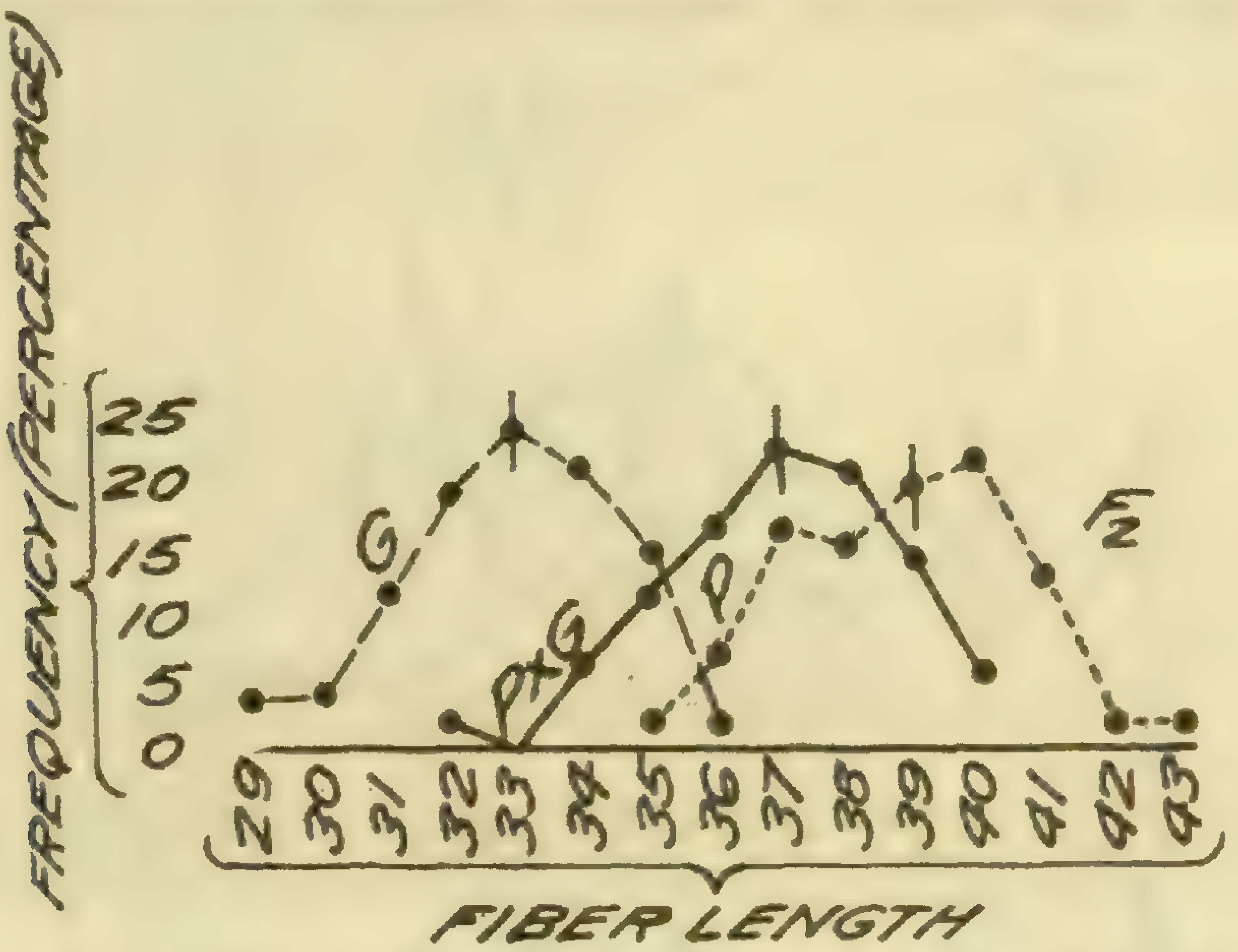


FIG. 3. Fiber length (mm.); second generation distributions of the parental and simple hybrid progenies. Details as in Fig. 1. The actual numbers of the respective populations were: Pima 46, Gila 53, P × G 49.

given by Balls (1909, p. 18) and by McLendon (1912, pp. 168, 169).[7] Yet in the Pima × Gila hybrids these characters behaved like the size and shape characters, showing unimodal distribution in the F_2. It should be noted, however, that in respect to these characters the differences between the two Egyptian varieties are much smaller than the differences between the parents of the wider crosses (Egyptian × Upland and Sea Island × Upland) dealt with by Balls and McLendon. Instead of the differences between pitted and smooth bolls, buff and white fiber and smooth and fuzzy seeds we have, in comparing Pima with Gila, merely the differences between more and less numerously and regularly pitted bolls, lighter and darker buff-colored fiber and more and less fuzz on the seeds.

[7] Complete dominance is apparently a rather rare phenomenon in cotton, even in the case of color characters. It is stated, however, by Leake and Prasad (1914, pp. 126–128) that yellow corolla color and the presence of the petal spot are completely dominant in certain hybrids of Indian cottons.

Correlation of Characters

It was sought to ascertain whether these hybrids show genetic as distinguished from merely physical or physiological correlations, in other words, whether there is coherence in the transmission of the parental characters. To this end, application was made of the test proposed by Collins (1916, p. 439), *i. e.*, comparison of the coefficients of correlation of the F_2 with those of the F_1. It is assumed that if the F_2 coefficient significantly exceeds that of the F_1, in the direction indicated by the relation of the parental means for the two characters, genetic correlation or coherence of characters is indicated. For example, the Pima parent has a lower leaf index and a higher boll index than the Gila parent. If there is coherence of these characters, the hybrid should show a negative correlation and the coefficient of correlation should be significantly larger in the F_2 than in the F_1.

The coefficients of correlation of 40 pairs of characters were determined for both the F_1 (grown in 1915) and F_2 (grown in 1916), upon the basis of one measurement of each character on each plant.[8] In three of these cases the coefficient of correlation of the F_2 was significantly larger than that of the F_1 (difference from 3.5 to 4.5 times its probable error), in the direction indicated by the parental relation. Since, however, the coefficients of correlation of the first generation (1915) and second generation (1916) of the parental progenies had also been found to differ in magnitude, the possibility was considered that the difference in the F_1 and F_2 hybrid coefficients was at least partly due to variations in the weather of the two years. The coefficients of correlation for the three character pairs above mentioned were therefore calculated for a new F_1 which was grown in the same year as the F_2.[9] When the F_2 and the new F_1 coefficients

[8] Two characters of great practical importance and in respect to which the parents differ very significantly, length of fiber and fuzziness of seeds, showed no significant correlations, either with each other or with the leaf and boll characters.

[9] The new F_1 was the result of crosses between daughters of the original parent plants, which had been made in 1915.

were compared, it was found that the former was significantly larger than the latter, in the indicated direction, for only one pair of characters (width of leaf and number of teeth on the involucral bracts) and in this case the difference was only 3.2 times its probable error.[10]

It was sought to throw further light upon this problem by determining the coefficient of correlation in the hybrid upon the basis of progenies rather than of individual plans. The means, for leaf index and boll index, of eleven F_3 hybrid progenies were used for this purpose. These progenies comprised from 8 to 44 plants each and the means were based upon measurement of one leaf and one boll on each plant. Since the Pima parent has the smaller leaf index and the larger boll index, the correlation in the hybrid, if determined by the parental relations of the two characters, should be negative. The coefficient obtained was in fact negative, but was no larger than its probable error ($r = -.17 \pm .18$).[11]

The balance of evidence is therefore strongly against the occurrence of coherence of characters in these hybrids between somewhat closely related, although distinct, varieties of cotton. It does not, of course, follow that the same result would have been obtained in the case of hybrids between less closely related types, especially if these differ in allelomorphic characters rather than in the variable size and shape characters which chiefly distinguished Pima from Gila.[12]

[10] The correlation in question, width of leaf with number of teeth on the involucral bracts, is doubtless physiological, large bracts being associated with large leaves and the number of teeth being greater on the larger bracts.

[11] The existence of an intervarietal correlation by no means implies that the same correlation will be found to obtain within a variety. For example, it is a matter of common observation that most varieties of cotton which have very long fiber have relatively sparse fiber, and vice versa. But when the correlation between fiber length and lint index (weight of fiber per 100 seeds) was plotted for 80 plants of the Pima variety, the value of r was found to be only .07 × .07, showing the complete absence of an intravarietal correlation.

[12] Instances of coherence of characters in hybrids of Egyptian with Upland cotton have been reported by Cook (1909, pp. 16, 17 and 1913, p. 53). On the other hand, Marshall (1915, pp. 57, 61), describing the F_2 of hybrids

The Back-Crossed Hybrids

The means of the ¾ back-crossed hybrids for nearly all characters showed departures from the midpoint of the parental means which were both significant and towards the mean of the respective preponderant parent (Pima or Gila). In the ⅞ back-crosses, the mean virtually coincided with those of the preponderant parent, as the following data show:

Progeny Means of:	Leaf Index	Boll Index
Pima	78.1 ± .14	173 ± .18
Pima ⅞ back-cross [(P × G) × P] × P	78.7 ± .63	179 ± .66
Gila ⅞ back-cross [(P × G) × G] × G	94.1 ± .47	153 ± .90
Gila	93.1 ± .47	156 ± .51

The distributions, for leaf index and boll index, of the Pima ⅞ back-cross, were embraced by those of Pima and the distributions of the Gila ⅞ back-cross were embraced by those of Gila. It is therefore apparent that twice back-crossing the simple hybrid with either of its parents has sufficed to eliminate the influence of the other parent in the expression of these characters.

Absence of Mutants

Careful examination, in 1916, of every plant in the F_2 progenies of the simple hybrids and in the ¾ back-cross progenies, showed only various recombinations of the Pima and Gila characters. A large majority of the simple hybrid plants were approximately intermediate, although occasional individuals showed a near approach to one or the other parent. Most of the back-cross plants, as compared with the simple hybrid individuals, showed clearly the preponderating influence of the ¾ parent, but few if any plants in the ¾ back-cross progenies could have been classed as wholly Pima or wholly Gila, the influence of the one-quarter parent being observable in the great majority of cases. No instance of

between the equally different Egyptian and Hindi cottons, states: "Nor was it possible to discover any general correlations or definite associations between any of the more important structural differences."

the occurrence of new or extra-parental characters was detected, although a few plants in the F_2 of the simple hybrid slightly exceeded the range of one or the other parent. Examination, in 1917, of the F_3 progenies of the simple hybrids, and of the 7/8 back-cross progenies also failed to reveal the occurrence of any extra-parental characters. Nor have any new characters been detected in the first, second or third generation progenies from selfed seed of the parent individuals. It is evident, therefore, that nothing in the nature of a mutant has yet appeared in any of these line-bred and hybrid stocks.

It was not, however, expected that mutants would be detected in these small progenies, which were grown for the purpose of studying, under controlled conditions, the behavior of the hybrids in the earlier generations and to provide seed for the growing of each stock on a more extensive scale. Statistical evidence regarding the production of mutants can scarcely be expected until much larger numbers of plants have been examined. The stocks resulting from repeated back-crossing should be especially interesting to study in regard to the occurrence of mutation.[13]

Conclusion

The investigation here described was undertaken in the endeavor to ascertain the conditions under which mutants are produced, in Egyptian cotton. Simple and back-crossed hybrids were made between two varieties (Pima and Gila) which differ significantly in numerous characters. Three generations of the hybrid progenies and of progenies from selfed seed of the parent individuals, were grown. No evidence of the appearance of

[13] "Variations toward Upland or Hindi characters arising in dilute hybrid stocks of Egyptian cotton have been found to yield progenies with more stable expression of characters than direct hybrids between Egyptian and Upland cotton. Such facts suggest the possibility of developing a new method of breeding by dilute hybridization. By the use of a small proportion of foreign blood as a means of inducing mutative variations in otherwise uniform stocks it may be possible to secure desired combinations of characters in more stable form than they can be obtained by direct hybridization." (Cook, 1913, p. 96.)

new characters was detected in any of these progenies, but since mutants in Egyptian cotton are comparatively rare, it will doubtless be necessary to examine much larger populations before definite conclusions can be drawn as to the occurrence of mutation in these stocks.

The principal interest of the data thus far obtained attaches to the behavior of hybrids between varieties belonging to the same general type, as compared with that of the hybrids between different species of *Gossypium*, which have hitherto been the principal subject of genetic investigation in this group of plants.

The varieties used in this investigation are distinguished chiefly by size and shape characters, although a few of the characters in which they differ significantly have been found to behave as allelomorphs in hybrids between less nearly related forms of *Gossypium*. The Pima $\times$ Gila hybrids, however, showed no evidence of segregation in definite ratios in respect to any of the characters measured. There was little or no evidence of dominance in the F_1, and the F_2 distributions were practically without exception unimodal. The means of the simple hybrid were in most cases intermediate between those of the parents. The result of twice back-crossing the simple hybrid upon either parent was to obliterate the expression of the characters of the other parent.

It could not be demonstrated that genetic correlation or coherence of characters occurs in these hybrids. Apparently all characters which are not correlated physically or physiologically are transmitted independently.

The second and third generations of the hybrids, as compared with the parents after two and three generations of selfing, were not more variable than Gila, and were only a little more variable than Pima. This fact is of practical importance in cotton breeding, since it points to the possibility of obtaining relatively stable and uniform recombinations of the desirable characters of varieties belonging to the same general type, although breeders have found this to be well nigh impossible in

wider crosses such as those of Egyptian (or Sea Island) with Upland cotton.

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GENETIC RELATIONS OF THE WINGED AND WINGLESS FORMS TO EACH OTHER AND TO THE SEXES IN THE APHID MACROSIPHUM SOLANIFOLII

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INTRODUCTION

LIFE cycles are known, in many aphid species, from field observations alone. A number of cycles have been determined from breeding experiments upon aphids in confinement. Often, however, these experiments appear not to have used the pedigree method. In the course of some work on the potato aphid, *Macrosiphum solanifolii*,[1] I observed indications of peculiarities in the genetic relations of the various forms to each other, which could be detected only by the pedigree method. Experiments designed to demonstrate these relations were instituted, with the results described in this paper.

Macrosiphum solanifolii, as observed in these experiments, comprises four kinds of individual: (1) the apterous viviparous female, which is green; (2) the alate viviparous female, which is also green; (3) the oviparous or sexual female, which is wingless and of a yellowish-green color until late in life, when the abdomen becomes filled with green eggs which impart a green color to the female herself; and (4) the male, which is winged and of a brown or brown and green color. Of these types of individual, the alate female can be recognized when a little more than half grown by her wing pads. The oviparous female has thickened brown hind tibiæ covered with sensoria, which are recognizable with the unaided eye, and which develop a few days before maturity. The male

[1] Identified by Dr. Edith M. Patch.

is usually, though not always, distinguishable at birth because of its pink or gray color, and those that are green at birth usually develop the gray or pink color within a few days. This color of the immature male has not, I believe, been recorded in the published descriptions of the species, and it is not impossible that it is a characteristic of certain parthenogenetic lines only.

Miss Patch (1915) has described a pink variety of each of the viviparous forms. I have never seen these in my experiments, though thousands of individuals have been examined, except in diseased animals which died shortly after discovery. The immature pink aphids in my experiments have all been males. The occurrence of pink females is probably a characteristic of certain parthenogenetic lines.

In my experiments the potato has been exclusively used as the host plant. These plants were reared in pots and were covered with lantern globes closed at the top with muslin.

EXPERIMENTS

Relation of Winged and Wingless Forms to Each Other

Experiment 293.—Starting with sister individuals, two lines were bred for three generations, one line from apterous parents exclusively, the other from alate parents only. As in the other experiments to be described, about a dozen adult females were placed together on a single plant, to become parents of the following generation. When they began to produce young, the latter were removed daily, or every two days, to young plants. Successive groups of young were placed on one plant until they seemed likely to become too crowded (usually not over 150 per plant), after which a new plant was used. As many as five plants were required in some cases to receive the young of one lot of parents. In the tables these plants are designated, in the columns headed "Host Plant," as first, second, third, etc. As the young aphids became adult they were removed and either used for further breeding or destroyed.

As a rule the parents for the following generation were taken from the first of the host plants, and were transferred to a young healthy plant, on which they produced their young.

This particular experiment was started in June from a stock whose stem mother hatched in the greenhouse in the preceding January. The line had passed through a sexual phase in that time, but had been preserved by a small number of viviparous females. In Table I the line from apterous parents is represented in the upper half of the table, the line from alate parents in the lower half. For the sake of comparison the totals are placed together at the bottom of the table.

TABLE I

Contrasting the Offspring of Apterous Parents and those of Alate Parents in the Aphid *Macrosiphum solanifolii*

Generation	Parents	Host Plant	Dates of Isolating Young	Offspring			
				Apterous Viviparous Females	Alate Viviparous Females	Oviparous (Sexual) Females	Males
I.....	Apterous	First	June 27–June 30	49	64	0	0
		Second	July 2	35	73	0	0
		Third	July 4–July 5	33	48	0	0
II....	Apterous	First	July 7–July 9	22	118	0	0
		Second	July 11	44	88	0	0
		Third	July 13	21	62	0	0
		Fourth	July 14–July 16	27	28	0	0
III...	Apterous	First	July 18–July 21	47	29	0	0
		Second	July 23	7	7	0	0
I.....	Alate	First	[June 28–July 2	110	21	0	0
		Second	July 4–July 6	32	2	0	0
II....	Alate	First	July 9–July 11	66	29	0	0
		Second	July 13–July 14	99	50	0	0
		Third	July 16–July 18	62	52	0	0
		Fourth	July 21	41	12	0	0
		Fifth	July 23	14	4	0	0
III...	Alate	First	July 21	80	23	0	0
		Second	July 23	35	6	0	0
		Third	July 24–July 26	5	3	0	0
Totals from apterous parents................				285	517	0	0
Totals from alate parents..................				544	202	0	0

There is a striking preponderance of winged offspring in the families of wingless parents, and a preponderance of wingless offspring from winged parents.

Experiment 294.—This was a repetition of the preceding experiment, in part simultaneous with it but of shorter duration. The method of conducting the experiment was the same as in the preceding experiment. Table II gives the results.

TABLE II

CONTRASTING TWO RELATED LINES OF *Macrosiphum solanifolii*, ONE REARED FROM APTEROUS PARENTS, THE OTHER FROM ALATE PARENTS

Generation	Parents	Host Plant	Dates of Isolating Young	Offspring			
				Apterous Viviparous Females	Alate Viviparous Females	Oviparous (Sexual) Females	Males
I.....	Apterous	First	July 7–July 9	22	118	0	0
		Second	July 11	44	88	0	0
		Third	July 13	21	62	0	0
		Fourth	July 14–July 16	27	28	0	0
II....	Apterous	First	July 18–July 21	47	29	0	0
		Second	July 23	7	7	0	0
I.....	Alate	First	July 7–July 9	98	58	0	0
		Second	July 11	93	67	0	0
		Third	July 13	62	18	0	0
		Fourth	July 14–July 16	66	46	0	0
		Fifth	July 18	17	3	0	0
II....	Alate	First	July 18	65	10	0	0
		Second	July 21	179	29	0	0
		Third	July 23–July 24	22	4	0	0
Totals from apterous parents				168	332	0	0
Totals from alate parents				602	235	0	0

The conclusion is the same as from Table I. Apterous parents give birth more largely to alate offspring, alate parents more largely to apterous offspring.

Relation of Winged and Wingless Forms to the Sexes

Experiment 303.—Just before the sexual phase of the cycle began a line from winged parents was started from a line being reared from wingless parents. In so far as the two were bred simultaneously their progeny are recorded in Table III.

Of the sexual offspring, the wingless parents produced exclusively males, while the wingless parents gave birth to a very large majority of sexual females. It may be

TABLE III

CONTRASTING THE PROGENY OF ALATE PARENTS WITH THE PROGENY OF APTEROUS PARENTS, WITH SPECIAL REFERENCE TO THE SEXUAL FORMS, IN THE APHID *Macrosiphum solanifolii*

Generation	Parents	Host Plant	Dates of Isolating Young	Offspring			
				Apterous Viviparous Females	Alate Viviparous Females	Oviparous (Sexual) Females	Males
I.....	Apterous	First	Sept. 7–Sept. 9	68	2	0	0
		Second	Sept. 11–Sept. 13	33	37	0	0
		Third	Sept. 15–Sept. 19	0	14	0	36
		Fourth	Sept. 21	0	0	0	11
II.....	Apterous	First	Sept. 21–Sept. 23	0	62	0	0
		Second	Sept. 25–Sept. 27	0	17	0	0
		Third	Sept. 29–Oct. 9	0	2	0	59
		Fourth	?	0	0	0	11
I.....	Alate	First	Sept. 17–Sept. 19	6	9	0	0
		Second	Sept. 21–Sept. 23	7	0	8	12
		Third	Sept. 25–Sept. 27	0	0	19	1
		Fourth	Sept. 29–Oct. 5	1	0	14	4
II....	Alate	First	Sept. 27–Sept. 29	0	0	27	0
		Second	Oct. 1–Oct. 7	0	0	62	0
		Third	Oct. 9	0	0	4	0
Totals from apterous parents				101	134	0	117
Totals from alate parents				14	9	134	17

also pointed out that the conclusion regarding the relation of the winged and wingless viviparous females to each other that was drawn from Tables I and II is confirmed in Table III.

Progressive Change in the Frequency of all the Forms in Successive Generations

Confirmation of the conclusions drawn from the preceding experiments is found in several lines which were designed to show the normal life cycle over a considerable period when each generation was derived from wingless parents. In addition, these lines show a progressive change in frequency of both the winged and wingless viviparous forms and of the sexes. Owing to this progressive change it was not possible to maintain uniform parentage, since in the late generations there were no apterous individuals from which to breed. The principal lines were obtained in the three following experiments.

Experiment 299.—This was a line reared from a wingless female obtained out of doors about August 10. It was reared in the laboratory. Table IV records this line.

TABLE IV

A PARTHENOGENETICALLY-PRODUCED LINE OF *Macrosiphum solanifolii*, PRODUCED IN THE MAIN BY WINGLESS PARENTS

Note (1) the gradual transition from wingless to winged viviparous females; (2) the transition from viviparous (parthenogenetic) reproduction to sexual reproduction; and (3) the fact that the males are produced mainly by wingless parents, the sexual females chiefly by winged parents. See Experiment 299.

Generation	Parents	Host Plant	Dates of Isolating Young	Offspring			
				Apterous Viviparous Females	Alate Viviparous Females	Oviparous (Sexual) Females	Males
I.....	Apterous	First	Aug. 24–Aug. 25	50	0	0	0
		Second	Aug. 27–Aug. 28	51	0	0	0
		Third	Aug. 30–Sept. 3	29	0	0	0
II....	Apterous	First	Sept. 1	93	0	0	0
		Second	Sept. 3	149	0	0	0
		Third	Sept. 5–Sept. 7	49	0	0	0
		Fourth	Sept. 5–Sept. 15	0	2	0	37
		Fifth	Sept. 9–Sept. 15	58	42	0	7
		Sixth	Sept. 17	4	1	0	0
III...	Apterous	First	Sept. 9–Sept. 11	57	17	0	0
		Second	Sept. 13–Sept. 17	9	13	0	7
		Third	Sept. 19	0	0	0	9
IV...	Apterous	First	Sept. 17–Sept. 19	13	86	0	0
		Second	Sept. 21–Sept. 23	1	30	1	13
		Third	Sept. 25–Sept. 27	0	0	0	15
		Fourth	Sept. 29–Oct. 10	0	0	0	11
V....	Apterous	First	Sept. 27	6	81	0	0
		Second	Sept. 29	0	34	0	0
		Third	Oct. 1–Oct. 3	0	2	14	44
		Fourth	Oct. 5–Oct. 7	0	0	2	39
		Fifth	Oct. 9–Oct. 16	0	0	0	25
VI...	Apterous	First	Oct. 7–Oct. 9	2	17	3	0
		Second	Oct. 11–Oct. 16	0	1	11	21
		Third	Oct. 20–Oct. 27	0	0	0	12
	Alate	First	Oct. 16–Oct. 25	0	0	24	0
		Second	Oct. 30–Nov. 6	0	0	4	0
VII ..	Apterous	First	Oct. 18–Oct. 30	0	5	11	3
		Second	Nov. 6	0	0	0	1
	Alate[2]	First	Oct. 18–Oct. 20	0	0	134	0
		Second	Oct. 23	0	0	101	0
		Third	Oct. 25–Oct. 27	0	0	44	0
		Fourth	Oct. 30–Nov. 6	0	0	18	0
VIII .	Alate[2]	First	Nov. 1–Nov. 3	0	0	50	0
		Second	Nov. 6	0	0	10	0
		Third	Nov. 10	0	0	3	0

[2] The alate parents in the seventh and eighth generations were offspring of apterous parents.

Experiment 298.—This line was derived from the same female as Experiment 299, but was reared in the greenhouse. See Table V.

TABLE V

A PARTHENOGENETICALLY PRODUCED LINE OF *Macrosiphum solanifolii*, PRODUCED CHIEFLY BY APTEROUS PARENTS.

The same transitions noted in Table IV are observable here on a smaller scale. See Experiment 298.

Generation	Parents	Host Plant	Dates of Isolating Young	Offspring			
				Apterous Viviparous Females	Alate Viviparous Females	Oviparous (Sexual) Females	Males
I.....	Apterous	First	Aug. 13	7	0	0	0
II....	Apterous	First	Aug. 15–Aug. 17	100	5	0	0
III...	Apterous	First	Aug. 24–Aug. 27	15	0	0	0
		Second	Aug. 28–Aug. 30	65	2	0	0
		Third	Sept. 1–Sept. 5	64	4	0	0
IV...	Apterous	First	Sept. 7–Sept. 9	68	2	0	0
		Second	Sept. 11–Sept. 13	33	37	0	0
		Third	Sept. 15–Sept. 19	0	14	0	36
		Fourth	Sept. 21	0	0	0	11
V....	Apterous	First	Sept. 21–Sept. 23	0	62	0	0
		Second	Sept. 25–Sept. 27	0	17	0	0
		Third	Sept. 29–Oct. 9	0	2	0	59
		Fourth	?	0	0	0	11
V ...	Alate	First	Oct. 13–Oct. 20	0	0	14	0
		Second	Oct. 23	0	0	4	0

Experiment 270.—The stem mother of this line hatched from a fertilized egg that was laid in the greenhouse in November and hatched in January. In March and April the line passed through a sexual phase, but a small number of viviparous females were produced during this period and by them the parthenogenetic line was continued. The families were not fully recorded until the latter part of May. Table VI includes only the records beginning May 28. Nine generations are there recorded as if an uninterrupted line, but an explanation is necessary. In the midst of the fifth generation the aphids began to die in large numbers for an unknown reason. In a few days every aphid out of hundreds was dead. Fortunately two or three aphids were found on a discarded plant in the greenhouse. Since only this one line had been reared in the greenhouse up to that time I felt

TABLE VI

A PARTHENOGENETIC LINE OF THE APHID *Macrosiphum solanifolii* REARED CHIEFLY FROM APTEROUS PARENTS

With certain irregularities the features mentioned in Table IV are recognizable here also. See Experiment 270.

Generation	Parents	Host Plant	Dates of Isolating Young	Offspring			
				Apterous Viviparous Females	Alate Viviparous Females	Oviparous (Sexual) Females	Males
I.....	Apterous	First	May 28–June 3	12	31	0	0
		Second	June 5–June 8	8	0	0	0
II....	Apterous	First	June 12–June 16	31	25	0	0
		Second	June 18–June 25	3	5	0	0
III...	Apterous	First	June 27–June 30	49	64	0	0
		Second	July 2	35	73	0	0
		Third	July 4–July 5	33	48	0	0
IV...	Apterous	First	July 7–July 9	22	118	0	0
		Second	July 11	44	88	0	0
		Third	July 13	21	62	0	0
		Fourth	July 14–July 16	27	28	0	0
V....	Apterous	First	July 18–July 21	47	29	0	0
		Second	July 23	7	7	0	0
VI...	Apterous	First	Aug. 17	7	0	0	0
VII..	Apterous	First	Sept. 1–Sept. 9	27	0	0	0
		Second	Sept. 11–Sept. 17	4	0	0	4
		Third	Sept. 19–Oct. 5	1	0	0	10
VIII .	Apterous	First	Sept. 21–Sept. 23	0	50	2	0
		Second	Sept. 25–Sept. 27	0	15	5	15
		Third	Sept. 29–Oct. 3	0	0	0	34
		Fourth	Oct. 5–Oct. 16	0	0	0	29
IX...	Alate	First	Oct. 11–Oct. 16	0	0	76	0
		Second	Oct. 18–Oct. 25	0	0	4	0

safe in assuming that these were of the same line. From one of them the sixth (?) and succeeding generations of Table VI were obtained.

Attention is directed in Tables IV, V, and VI to the following points:

1. The wingless viviparous females, more abundant early in the cycle, are gradually replaced by winged females. This is especially clear in Tables IV and V. It is obscured in Table VI by the fact that this line is not really a continuous one. A catastrophe in the fifth generation made it necessary to resume this line by means of a female from the same stock. Up to the fifth generation there is an irregular increase in the proportion of winged females, which reaches its climax in the fourth

generation. It is impossible to state what the fifth generation would have included, since only one fifth of the probable progeny were produced or survived. After the fifth generation up to the complete disappearance of viviparous forms, there was again a replacement—this time rather sudden than gradual—of the wingless females by winged ones. The same gradual disappearance of wingless viviparous in favor of winged females was observed in several other experiments of shorter duration which are not included in this paper, and has also been found in *Microsiphum destructor* by Miss Gregory (1917). It is therefore to be regarded as of general occurrence.

2. There is observed in two of the tables (IV and VI) a gradual increase in the tendency of wingless females to produce sexual females instead of males, as they most often do when the sexual phase begins. Thus in Table IV, generation IV, 2.5 per cent. of the sexual forms produced by apterous parents were sexual females. In generation V, 12.9 per cent. of the sexual forms were females. In the sixth generation, of the sexual offspring of apterous parents, 29.7 per cent. were females. In the seventh generation, which is the last from apterous parents, 73.3 per cent. of the sexual offspring were females. Thus, while the apterous parents produced mostly males during the sexual phase, there is a gradually increasing tendency to produce females. In Table VI is a brief indication of this same phenomenon. Males alone (of the sexual individuals) appear in the seventh generation, but a small number of females in the eighth generation. Unfortunately no apterous parents were available for a further generation. If it were possible to obtain wingless females in later generations it would be interesting to note whether they would not eventually produce only females.

Whether there is a similar progressive change in the sexual offspring of winged females is not so clear, since in none of the last three tables of this paper are there any male offspring of alate parents. However, in the

lower half of Table III there is an example of this kind. In the first generation from alate parents there is a minority of males; in the second generation no males. It is not improbable that, if a long line had been bred from alate parents, there would be a progressive decrease in the proportion of male offspring in the sexual phase of the cycle.

3. Tables IV, V, and VI also contain confirmation of the conclusion drawn from the earlier tables, namely, that at any given time winged viviparous parents produce more wingless viviparous offspring than do wingless parents, and that in the sexual phase males are produced chiefly by the wingless parents, sexual females by winged parents.

Discussion

Although the most striking results of the foregoing experiments may appear to be the fact that winged viviparous females produce mostly wingless females in the parthenogenetic part of the cycle and sexual females in the sexual part, whereas the wingless viviparous females produce chiefly winged females in the parthenogenetic phase and males in the sexual, nevertheless the clue to the explanation of this phenomenon is more nearly discoverable in the progressive change in the frequency with which all forms occur in successive generations. Thus, there is a transition from a preponderance of apterous females early in the cycle to a predominance of winged females later. There is likewise, in the sexual portion of the cycle, a transition from males to sexual females. This latter transition has been demonstrated in the offspring of wingless mothers, and is indicated as probable in the offspring of winged females.

These transitions imply a gradual change of some sort, presumably in the metabolism of the animals. While the difference between a male and a sexual female, or between an apterous and an alate viviparous female, may be a definite morphological difference such as a difference in chromosomes, so that an individual is either the one or

the other, not an intermediate, it is hardly possible to escape the conclusion that the thing which brings about or prevents the morphological alteration is a gradual process. What this gradual change may be in the present case can not be known from the evidence, for obviously changes in the type of metabolism may be of various kinds.

Riddle (1917) conceives of such a change of metabolism as a change from individuals having a high rate of metabolism and low energy content to individuals having a low rate of metabolism and high energy content. In the eggs of pigeons forced to lay eggs continuously, he finds just such a change. The early eggs are of the former type, the late eggs of the latter type. From the early eggs are developed males, from the late ones females; and on those facts, supported by other work, Riddle bases an elaboration of the Geddes and Thompson theory of sex.

An attempt has been made to fit the facts obtained from aphids to Riddle's conception of sex. The gradual transition that occurs both in the parthenogenetic and in the sexual phase of the cycle of *Macrosiphum* indicates that one type of metabolism is prevalent early in the cycle, and the contrasted type late in the cycle. The fact that in this transition males precede sexual females shows that, if Riddle's hypothesis holds for the aphids, the progressive change is from a high rate of metabolism and low energy content to a low rate of metabolism and high energy content. Now it has been shown that wingless viviparous females precede winged ones, the change from the one form to the other taking place in part simultaneously with the transition from males to sexual females. Hence in accordance with Riddle's scheme wingless females should represent a high rate of metabolism and low energy content, while the winged ones should possess a low rate of metabolism and high energy content. With regard to the rate of metabolism alone, this assumption is supported by the fact that winged females require longer

to develop, that they produce fewer young per day, and that these young are on the average smaller than in the case of wingless females.

There are certain objections, however, to the foregoing conclusion. First, if winged viviparous females have a low metabolic rate while the wingless ones have a high rate, during the parthenogenetic portion of the cycle a parent with high rate of metabolism produces chiefly offspring with a low rate of metabolism, and *vice versa;* for wingless females produce chiefly winged ones, and winged females produce chiefly wingless ones. On the other hand, in the sexual part of the cycle, parent and offspring are both of the same metabolic type; for winged females (with low rate of metabolism) produce mostly sexual females (which in accordance with Riddle's view should possess a low rate of metabolism), whereas wingless females (high rate) produce mostly males (high rate). Why parent and offspring should be of a similar type of metabolism in the sexual phase, but of unlike type in the parthenogenetic phase, is not clear.

Unless the withholding of food increases the rate of metabolism, or unless the rate of metabolism is taken to mean not the absolute rate, but the rate relative to the food consumed, another objection to the assumption that the winged female possesses a lower rate of metabolism than the wingless ones is found in the work of Miss Gregory (1917). Miss Gregory finds that in *Microsiphum destructor* starvation of the apterous mothers results in the production of more winged offspring. It is only by assuming that starvation increases the rate of metabolism, or that "rate of metabolism" means the relative rate—rate relative to the amount of food consumed, not relative to the rate in another type of individual—that Miss Gregory's discoveries can be interpreted in support of Riddle's hypothesis; providing, of course, that the winged females have a lower metabolic rate than the wingless females.

If, to avoid either or both of the difficulties just men-

tioned, and notwithstanding the slower development, smaller young and smaller daily output of young of the alate females, these winged individuals be assumed to have a higher rate of metabolism than the wingless ones, other difficulties are encountered. This assumption would have the advantage of allowing parent and offspring to be of opposite metabolic type in both the parthenogenetic and sexual portions of the cycle, instead of being of opposite type in the parthenogenetic phase and of like type in the sexual phase. The transitions, however, would be in opposite directions in different parts of the cycle. In the parthenogenetic portion there would be a transition from a low rate of metabolism to a high rate (wingless to winged); while in the sexual part of the cycle the transition would be from high rate to low rate (male to sexual female). These opposite transitions would have to occur in part simultaneously, as in Table IV, fourth and fifth generations.

Unfortunately there has been no opportunity to determine experimentally the rate of metabolism in the various kinds of individuals in *Macrosiphum;* that is part of the program for the future. In the meantime, whether there is a fallacy in the foregoing argument, or a fallacy in Riddle's conception of the relation of metabolism to sex, can not be asserted with any degree of confidence.

Obviously the mere rate is not the only feature of metabolism that may conceivably be related to sex. If there are qualitative differences in the reactions that constitute metabolism, it seems to me more likely that these would influence the development of sexual organs than that the production of ovaries rather than testes could be determined by rate of metabolism alone. Qualitative differences in the reactions might entail differences in the rate of CO_2 production, and therefore be interpreted as quantitative differences. An increase in the output of lumber from a sawmill might be taken to indicate that the saws were running faster than formerly, whereas in reality the saws had been replaced by a new type of saw.

So long as rate of metabolism can be determined experimentally, while the precise reactions can not, there is every reason to continue the attempt to relate the rate of reaction to the course of development. But when facts come to light which do not easily fit preconceived ideas, it is highly important that alternate possibilities be kept in mind.

It is not impossible that the difficulties discussed above may be removed by discovering that the metabolic change that causes the transition from wingless to winged females is different from the change that causes the transition from males to sexual females. The two changes may be more or less independent of each other. In that case it may be possible to separate them experimentally. An agent may sometimes be found which will hasten or postpone the sexual reproduction without in any way affecting the transition from wingless to winged females in the parthenogenetic phase. If this agent hastened the sexual reproduction, it should act as a male-producing factor, since sexual forms would be introduced while wingless parthenogenetic females were more abundant. If, on the other hand, the agent delayed sexual reproduction, it should favor females, since the parthenogenetic mothers would then be more largely winged.

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ORGANIC EVOLUTION AND THE SIGNIFICANCE OF SOME NEW EVIDENCE BEARING ON THE PROBLEM

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I

THE biological problem recognized as having the greatest fundamental importance at the present period is that problem of evolution relating to the means by which the heritable characters differentiating various organisms from one another were first called into existence, or granting the validity of the gene hypothesis and speaking more concisely, how hereditary character-forming genes have originated in the process of evolution. That the diverse forms of life found upon the earth are only to be explained as the result of organic evolution, is a proposition which scarcely needs be mentioned at the present period in the history of science, at least so far as individuals endowed with minds reasonably logical in evaluating evidence are concerned. It is not evolution as a process going on in the world which is being particularly questioned nor the general method by which characters once having originated are inherited, but the particular method by which heritable characters first arose.

The purpose of the essay here presented is threefold. *First,* that of pointing out the unsatisfactory nature of much of the earlier evidence as a basis for sound generalizations in connection with a clear understanding of evolution. *Second,* that of calling attention to the serious shortcomings of modern methodology in throwing light on the causative factors of evolution. *Third,* that of presenting some new evidence somewhat unique in its nature, based in part on preliminary experimental work, to

the effect that the environment acting through long intervals of time may impress characters upon an organism which become unalterable by reversal processes.

To these propositions may be added the suggestion of the fundamental importance which physico-chemical methods must play during the future in solving the problems of evolution.

II

The controversies relating to evolution have been many. When, however, one considers the interest attached to the subject, its broad bearing on various phases of human welfare—sociology and economics in general, animal and plant breeding in particular—together with the difficulties of interpretation which apparently have increased rather than diminished during the sixty or more years seriously devoted to its elucidation, it is not at all surprising that many different conclusions have been reached, many dogmatic statements presented, and many acrimonious discussions engendered.

In connection with a clearer understanding of the points at issue, it will be well to pass certain historical details relating to the development of the different theories somewhat critically in review. This is done even at the risk of a repetition of facts quite familiar to those who have taken more than a passing interest in the subject.

For long the theory of natural selection dependent on the inheritance of small chance variations received general acceptance. Championed by Weismann in his notable controversy with Spencer to the exclusion of the Lamarckian idea that characters acquired through environmental stimuli were heritable, it seemed at the time entirely plausible as an explanation meeting the conditions.

With the greater attention given to experimental methods, however, doubt arose concerning the fundamental value of selection and resulted in the presentation of the mutation theory by DeVries. Here evolution was inter-

preted as arising from sudden and comparatively extreme variations passed on by inheritance in nearly an unchanged condition. Once more the results of experimental work along the lines of the rediscovered principle of Mendelian segregation indicated to a large number of students of evolution that the facts set forth by DeVries were subject to quite another explanation, in itself having no bearing on the origin, but merely on the redistribution of the character-forming units already present in the stock utilized. Another explanation not taking into account the purity or impurity of the parental stock, accounted for "mutations" through the sudden ineffectiveness or loss of a gene.

The dissatisfaction thus arising resulted in the return of many to the fold of "acquired characters." Semon (1912) reviving the "mneme" principle received the support of Wettstein, Przibram, and others. A disinclination existed, however, among most naturalists to accept the evidence presented as seriously upholding the inheritance of new characters produced by environmental stimuli. Explanations of the results on quite other grounds seemed more plausible. For example, the work of Tower (1906), (1910), etc., in attempting to control the color pattern of the potato beetle by changes in temperature and humidity, encountered the impurity of the germplasm objection as well as the gene loss objection, either one of which would be fatal to the validity of the conclusions, if sustained. Commenced at a period in 1895, prior to the rediscovery of the principles dealing with alternative inheritance, and finished in 1904 before the facts were duly appreciated, it is not at all improbable that genetic complications in the way of recessives, modifiers, losses, lethals, etc., were involved. The destructive criticism presented by Cockerell, Gortner, Bateson, Castle, and others, particularly in reference to the later studies of Tower (1910), makes it evident that the results must be confirmed from independent sources with more consideration to the possible errors mentioned before the conclusions are to be accepted.

Similarly, the work of MacDougal (1907), in connection with the modification of *Raimannia odorata,* one of the Patagonian primroses, may be explained. Compton, as noted by Bateson (1912), using the same species, was unable to obtain like results, while Humbert (1911) utilizing 7,500 pure line plants of *Silene noctiflora,* one of the "pinks" also failed to obtain so-called "mutants" similar to those found by MacDougal.

The investigations of Kammerer, Woltereck, Ferroniere, etc., are of decided interest, but to those critically inclined they offer no evidence giving pronounced support to the proposition that environmental stimuli form new genetic factors.

Thus, in turn, have the theories as to the method by which evolutionary progress occurs been undermined by doubt. Feeling the insufficiency of small chance variations, of environmental variations, and of larger germinal variations, as a summation process, it is not to be wondered that the truth-seeking pilgrim has become wearied in his journey and longs for a more secure resting place.

III

Let us return to the problem as suggested in the opening paragraph, namely the actual origin of heritable characters, and consider somewhat more carefully as to whether theories exist justified by facts, which will furnish acceptable evidence. There are two well-developed hypotheses, the general one of DeVries and the more specific one of Morgan and his associates, founded on discontinuous variations, and that of Castle based on continuous variations.

Considering the views of DeVries and his followers in the light of experimental investigations made during the last ten years, it has become more and more evident that by far the greater number, if not all, of the so-called mutations thus obtained, were explainable on the basis of the combinations of preexisting units of the germ cells. This rests upon the proposition that there are present in the

gametes certain hypothetical entities to which the name gene or factor has been applied and which give rise to the heritable characters of an organism. Thus it is at once recognized that the problem relates to the origin of the gene, rather than to the origin of the apparent characters with which it is correlated, and that by far the greater number of so-called new characters are not new, but were performed at remote periods of time. So far as the present arguments are concerned, it matters not whether the results are assumed to be brought about by material units or enzyme reactions. The prepared potentialities exist in either case.

As examples of extreme types of characters which may arise from the combinations of existing genes and which might have been considered "mutations" at an earlier period when the facts as to their origin were not fully known, one need only mention the "blue" of the Andalusian Fowl exhibited by the hybrid between the black and white parental stock, or the "pink" presented by the cross between the red and white "four-o-clocks" of Correns. A type of characters more in line with mutations which have been described and to which there is every reason for believing that many of them may be referred, rests upon multiple gene effects combined with sterility, in accordance with evidence presented by Davis, and others. Of decided interest in this connection is a recent paper by Muller (1917) calling attention to "An *Œnothera*-like case in *Drosophila*" where a result quite comparable to certain mutations of *Œnothera* is explained through the action of balanced lethal genes. There are other varying degrees of combinations from which "mutant" characters may arise and which depend on the behavior of the genetic material in connection with recessives, modifiers, lethals, crossovers, non-disjunction, etc.

There is really nothing extraordinary in the appearance and disappearance of the characters thus formed, beyond their interpretation, and this has furnished false premises for many erroneous conclusions, chief of which,

in the opinion of the writer, is the mutation theory as outlined by DeVries in so far as it may account for progressive evolution.

Inasmuch as it seems probable that the results obtained by Castle are to be explained upon the same basis as those of DeVries, it will be well to consider them in this connection. Here it is assumed that a continuously variable heritable gene is involved, and that progressive results are obtained through the selection of the "unit characters" produced by such a gene. Castle, however, stands almost alone in vigorous support of such a variation, while opposed to him are the Hagedoorns, Morgan, Pearl, Punnett, McDowell, Muller and others equally insistent that genes once having originated pass on from one generation to another unchanged except in comparatively rare instances where so-called "mutations" occur.[1] It is maintained by those advocating this view that the results in connection with hooded rats on which Castle bases his contentions, are due to an uncertain number of modifying genes not in themselves variable, and that the existence of such genes has been demonstrated in other organisms presenting results similar to those obtained in rats. The work of Little (1917) with mice where three segregating types of spotting were found to produce varying degrees of color pattern, indicates that multiple genes are involved. Furthermore, the analysis by Little of the data obtained by Castle, Phillips and Wright, points decidedly to the interpretation of their

[1] Jennings (1917) has recently endeavored to show that the views of Castle and his opponents are identical. This, however, is by no means the case. On the one hand there is the idea of a continually variable gene (coat-color-producing gene in rats) moved gradually along a given scale by selection. On the other hand there is the idea of a rarely mutating gene (*e. g.*, sex-limited eye color producing gene in *Drosophila*) moving abruptly from one part to another of the scale. Its position once obtained remains for a long time constant. These differences of interpretation are at present irreconcilable.

Since this note was written, Morgan (1917) has discussed the matter in detail, presenting arguments quite similar to those mentioned above, and arriving at a similar conclusion.

results on the basis of multiple genes instead of a continually varying gene.

It would thus appear evident that the theory outlined by Castle is open to quite the same objections that occur in connection with the mutation theory of DeVries, and that there is little evidence for believing that it has any fundamental value in explaining evolution.

The mutation theory of Morgan and his associates, based primarily on results obtained in studies of the small "fruit-fly" *Drosophila,* apparently presents quite another view of the subject. Here it is clearly indicated that evolution has taken place through the incorporation of mutant changes, and that these changes are due to discontinuous "mutations" of genes as exemplified in multiple allelomorphs.

Assuming the validity of the arguments based on linkage relations in respect to the localization of the genes, the conclusion follows that the "mutation" results either (1) from a change in a specific gene or (2) from the complete linkage of a series of genes. If the latter proposition should be the correct interpretation, and it is by no means clear that it is not, the objections urged against the theories of DeVries and of Castle hold equally here.

Morgan and several others have presented evidence for believing in the specific change of a gene. Granting that this is the actual explanation of the facts presented in connection with multiple allelomorphs, etc., there are two lines of argument leading to the conclusion that these changes are results of combinational sub-units or subgenes existing in the species, and that progressive evolutionary changes are no more represented here than in the previous theories of DeVries and of Castle.

The first argument (*a*) rests upon the recurrent "mutations" which have been noted in a considerable number of cases. Thus the sex-linked eye colors of *Drosophila* forming the multiple allelomorph system consisting of white, eosin, cherry, blood, tinged, and buff, and their dominant allelomorph, red, of the wild fly, have their

origin from a single definite area or locus in the "X" chromosome, accepting linkage as a criterion. They have not arisen in a continuous series but as sudden changes from one extreme to another at comparatively long intervals. The character may remain modified in one direction and then suddenly revert to an original condition. Thus white changed to eosin and later back to white as noted by Morgan (1916). Furthermore, the changes are not extremely infrequent. A similar transformation has been noted by Emerson (1917) in maize where self color apparently changed to variegation and later back to self color. A variation which may be of the same type has been described by Shull (1911) for *Lychnis*. Quite recently Zeleny (1917) in studies on *Drosophila melanogaster* Meig. (=*ampelophila* Löw)[2] has noted a reversed mutation where full-eyed flies result from the return of the bar gene to the original full-eyed condition. In each of the cases mentioned the germinal purity of the stock was believed to be without question.

Such results are not to be attributed to a continuous series of mutations, to progressive changes, or to genetic losses. They clearly suggest that the gene, if it is the individual gene which is involved, is made up of smaller combinational units which through their permutations give rise to the characters in question. Presumptive evidence is certainly furnished against the idea that anything new has developed in the organism to form the particular characters. Furthermore, one may well believe that any particular mutation under observation sufficiently long, will exhibit recurrent changes.

The second argument (*b*), to the effect that the gene is comparatively stable and that "mutations" are only transitory combinational changes, is based on the maintenance of apparently identical genes through long periods of time. Thus Metz (1917) found that the three mutations which had, up to that time, occurred in *Drosophila virilis* Sturt. appeared exact duplications of the

[2] Sturtevant, mss.

mutations in *Drosophila melanogaster* Meig.[3] In both species "confluent," a modification of the wing venation, is similar in form, dominant over "normal" and "lethal," when the fly is homozygous for the character. The characters "yellow" and "forked" are sex linked in both species and otherwise alike so far as the evidence exists. Inasmuch as the earliest representative of *Drosophila* thus far known is a species not decidedly different from those now existing as noted by Löw (1850), who described it from the amber of the Baltic Sea, and belongs to the Lower Oligocene of the Tertiary Period, with an age of from two millions to three millions of years, one must infer that the genes common to the two species mentioned have been preformed for a long period of time, and that nature has paid little attention to such mutational changes as occur in connection with multiple allelomorphs.

There are certain investigations widely separated as to their content, but apparently closely correlated as to the underlying explanatory principles involved, which must not be overlooked in a consideration of the changes which may take place in hereditary units. These are concerned with the differences involved in metabolism.[4]

On the one hand there are studies dealing with the direct effects of a changed metabolism on the developing individual. Here may be mentioned the work of Lillie in connection with the "free-martin" of cattle; Steinach on the transplantation of the gonads in rats and guinea-pigs; Goodale on the grafting of ovaries in male fowls; Pearl and Surface on the degeneration of the ovary in cattle; Riddle with pigeons, etc. On the other hand, there are studies dealing with the indirect effects on inheri-

[3] The species are distinctly separated not only in external appearance but also by their chromosome number. *D. melanogaster* has four pairs, while *D. virilis* has five pairs of chromosomes.

[4] The theory has had a long historical development. Treat (1873) published a paper on controlling sex in butterflies as a result of food supply. Yung (1881) worked with tadpoles. Nussbaum (1897) with rotifers. Recent evidence of an elaborate nature has been presented by Goldschmidt, Woltereck, Whitney, Banta, Shull and others.

tance. Among these may be mentioned that of Goldschmidt with moths; Woltereck with daphnids; Plough with temperature effects on *Drosophila*; Hoge with the effects of cold on *Drosophila*; Morgan with the effects of moist food supply on *Drosophila*, etc.

As an example of the development group, the investigation of Lillie may be noted. The evidence obtained showed that the "free-martin" or sterile female usually developing where the twins are of separate sexes in cattle, etc., resulted from the modifying influences of the sex hormones in the male where the two chorions had anastomosed.

As an example of the inheritance group, Morgan has found that the "mutant" "abnormal abdomen" in *Drosophila* occurs in connection with a moist food supply. The character is a sex-linked dominant. If an abnormal male is bred to a normal female and the food is kept moist, the sons are normal and the daughters abnormal. If the food is dry both sons and daughters are normal. The reciprocal cross gives sons and daughters both abnormal with moist food but normal with dry food.

It follows then that in *Drosophila* the gene for the abnormality—or the chemical preparedness for the inhibition of normality, if one so wishes to term it—is performed in the "X" chromosome and merely awaits a suitable environment before presenting itself as a character. Similarly, in connection with the changes occurring in the development of the "free-martin" of cattle, it seems necessary to admit that there are genes present in the sex chromosome concerned with the development of sexual characters which, however, are in a state of equilibrium, and that the inhibition or the excitation[5] of one or the other genes or groups of genes will result in the development of the corresponding individual.

From the facts presented, one seems justified in making the deduction that heredity hands down a framework

[5] It has been shown by Chapin (1917) that the gonads of the free-martin originally destined to be a female, attain a male condition.

which within certain limits allows a plasticity in the development, and that the direction of development is determined by physico-chemical influences through the suppression of potential units.

Thus the conclusion seems almost unavoidable that by far the larger number, if not all, of the heritable characters making up an organism, result from combinational units which have long been predetermined, and that the breeder, whether the semi-scientific agriculturist or the ultra-scientific drosophilist, is largely, if not entirely, engaged in presenting new combinations of existing units. If this be true, modern genetics has left the actual problem of evolution far to one side and deals only with results of a secondary, although none the less interesting, nature.

One is, therefore, led to inquire as to whether there may be available evidence which will permit a new insight into conditions governing the formation of characters, even though the evidence from its nature must be largely circumstantial.

IV

Accompanying the progressive swimming movement of most aquatic microorganisms there is a characteristic axial rotation. This has been noted by Nägeli, Engelmann, Strassburger, Mast and more in detail by Jennings (1901) who has called attention to the value which such a compensatory motion may have for the organism in which it exists. No explanation has been suggested other than this as to the origin of the rotation, and without further thought it is evident that one would be inclined to attribute it to natural selection, assuming that those individuals in which it did not occur were at a disadvantage in the struggle for existence by reason of their more confined movement.

It is the phase of the question dealing with the particular causes bringing about the rotation that appears to be of extreme significance when considered in connection with the principles underlying evolution and to be

susceptible to quite another explanation than the natural selection implied by the term "adaptiveness" which, in accordance with Jennings (1906), is based on the idea that "it tends to preserve the life of the animal." Furthermore, when the groups of facts associated with the characteristic rotation are brought in review, it would seem that the explanation suggested may go far toward interpreting the origin of the fundamental activities as well as the origin of the characters in general of organisms.

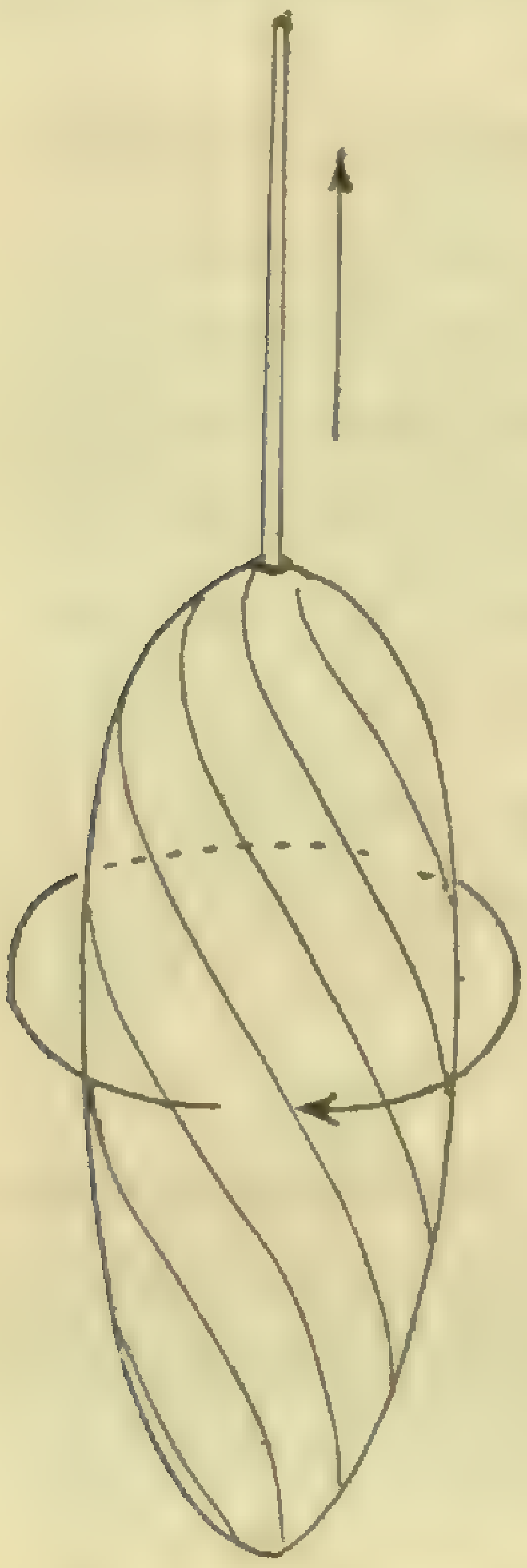


FIG. 1. Typical Euglenoid Flagellate illustrating left-hand spiral arrangement of striæ in connection with clockwise rotation (observer in front) and progressive movement by means of anterior flagellum.

In connection with the preparation of a systematic review of the order Euglenoidina belonging to the class Flagellata of the Protozoa (1915), it was noted with decided interest that a large number of the forms possessed an oblique striation ranging from almost indiscernible markings to characters of great complexity impressed upon a cellulose-like envelope (*e. g.*, *Euglena spirogyra* Ehrenb., *Phacus pyrum* (Ehrenb.), *Heteronema spirale* Klebs, etc.), the striæ extending forward and to the left. The character also appeared to be invariably correlated with an axial rotation of the organism from right over to left (Fig. 1). Such a movement is to be described in physical terms as "clockwise," the position of the observer being in front of the advancing organism.

The facts took on additional interest when it was noted that forms with a reverse striation seemed entirely absent from the northern hemisphere, although such forms existed in the southern hemisphere.

Inasmuch as the euglenoids are in general positively phototactic under normal conditions, it would immediately occur to one seriously considering the question, that

the underlying principle producing the rotation was the turning of the earth on its axis, with the resultant apparent motion of the sun from east to west. Such a hypothesis would become the more tenable when it was found that negatively phototactic microorganisms of the northern hemisphere rotated as a rule in a reverse or counter-clockwise direction.

Some of the evidence thus far obtained may be presented more clearly in tabular form[6] (Table I). Thus

TABLE I

A series of aquatic microorganisms showing in general the clockwise rotation of positively phototactic forms and the counter-clockwise rotation of negatively phototactic forms in the northern hemisphere, with evidence for the tendency to reverse condition in the southern hemisphere.

Northern Hemisphere		
Euglena viridis Ehr.	Positive.	Clockwise.
Euglena hæmogranulata Walt.	Positive.	Clockwise.
Euglena tripteris Duj.	Positive.	Clockwise.
Euglena spirogyra Ehr.	Positive.	Clockwise.
Leptocinclis ovum (Ehr.)	Positive.	Clockwise.
Phacus pyrum (Ehr.)	Positive.	Clockwise.
Cryptomonas ovata Ehr.	Positive.	Clockwise.
Pandorina morum (Müll.)	Positive.	Clockwise.
Eudorina elegans (Ehr.)	Positive.	Clockwise.
Volvox globator (Linn.)	Positive.	Clockwise.
Stentor polymorphus Ehr. (=*viridis*)	Positive.	Counterclockwise.
Phacus longicauda Ehr.	Positive.	Counterclockwise.
Stentor cœrulus Ehr.	Negative.	Counterclockwise.
Anurea cochlearis Gosse	Negative.	Counterclockwise.
Arenicola cristata (larva)	Negative.	Counterclockwise.
Chilomonas paramæcium Ehr.[1]	Negative.	Counterclockwise.
Southern Hemisphere		
Leptocinclis piriformis Cun.	Positive?	Counterclockwise.
Phacus bacillifer Cun.	Positive?	Counterclockwise.
Leptocinclis mammilata Cun.	Positive?	Clockwise.

it may be stated that so far as the facts are available, positively phototactic forms with the exception of

[6] The rotation direction and light responses noted are those taking place under normal conditions. The conclusions presented are not altered by the fact that as a result of stimuli under conditions imperfectly known, reverse movements may occur, *e. g.*, the negative response of Euglenoids to intense light.

Stentor polymorphus Ehrenb. (=*S. viridis* aut.) and *Phacus longicauda* Ehrenb. rotate clockwise in the northern hemisphere. Inasmuch as the phototactic relation of the ciliates in general is negative, where a reaction exists, it seems probable that the inclusion of the minute symbiotic forms of algæ, *Chlorella vulgaris* Beyer, which gives the species its characteristic green apperance, has induced a change from a negatively phototactic to a positively phototactic condition, while the organism retained its original counterclockwise rotation. Small forms like *Chlorella* which contain chloroplasts, are generally positively phototactic so far as their responses to normal conditions are known.

Phacus longicauda (Ehrenb.) is an euglenoid about 100 μ in length, with comparatively flat wing-like expansions. The striæ covering the body are longitudinal. In swimming, however, many of the forms have the anterior part of the right expansion turned slightly down, while the left expansion is turned up in a similar manner. This gives their progressive movement a counterclockwise rotation.

In the southern hemisphere direct observation of the characteristic rotation has not been made, but inasmuch as the direction of the striæ indicates the direction of the rotation, certain evidence is available. Cunha (1913) in his studies of Protozoa from Brazil has figured several forms showing distinctly the arrangement of the striæ in the excellent plates drawn by himself. While it is not impossible that a careless investigator might focus on the lower part of the specimen, thus showing the reverse position of the striæ, the careful work of Cunha scarcely permits one to suggest such a criticism. It may furthermore be noted that the apparently counterclockwise rotating forms described by him are species quite different from the typical northern forms, while the forms which evidently rotate clockwise are closely allied to species from the northern hemisphere, and may have been introduced comparatively recently so far as evolutionary time is concerned.

The original development of the unicellular forms in the northern hemisphere with their subsequent introduction to the southern hemisphere by aquatic birds, etc., is well within the range of possibility and suggests that even should forms with reverse rotations be entirely absent from south of the equator, the hypothesis which has been proposed would by no means be invalidated.

Having presented the general facts as to the behavior of free-swimming microorganisms, it becomes advisable to consider the explanations which may exist as to the origin of the characteristic rotation. It seems impossible to attempt to account for such a character on the ground of "natural selection." One would be compelled to believe that the reverse rotation—the counterclockwise rotation of positive northern forms—possessed an elimination value, an almost indefensible proposition, particularly when forms like *Stentor polymorphus* and *Phacus longicauda* are considered as well as forms in the southern hemisphere which do not rotate in agreement with theory.

The most obvious explanation to be considered is that based on the influence which the sun in its apparent daily movement from east to west in the equatorial region may be supposed to have exerted on the flagellum (Fig. 2). This assumes that the flagellum is the orienting factor and that the sun has induced in it an east-west rotary-like or whip-like propelling movement. The consequent mechanical effect would be that in the northern hemisphere forms with a positive light reaction would rotate clockwise and those with a negative light reaction would rotate counterclockwise. Conditions would be reversed for those which might be present in the southern hemisphere during the evolutionary stage.

Conversely, negatively phototactic forms would develop a reversed or counterclockwise rotation by means of the influence of the light rays on the stroke of the light avoiding flagellum and their modified organs, the cilia. It is by no means necessary to believe that the stroke of

the flagellum should be one of rotation, although theory would imply a partial rotation in the primitive flagellate forms. The method of movement by means of the flagellum furnishes a problem of considerable difficulty which

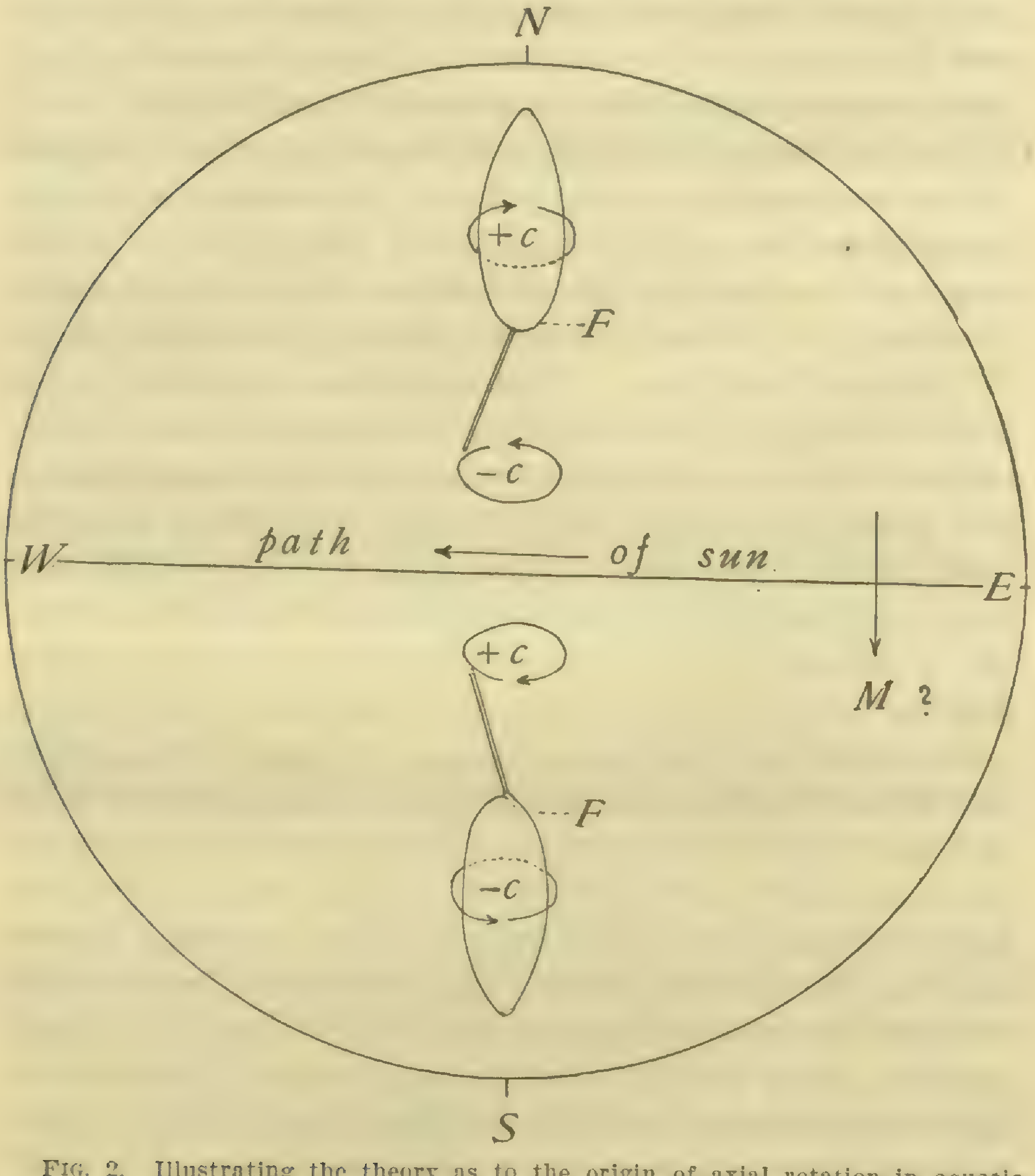


FIG. 2. Illustrating the theory as to the origin of axial rotation in aquatic microorganisms of the northern and southern hemisphere of the earth by the apparent movement of the sun from east to west. *N*, etc., north, etc.; *F*, flagellate organism; **+ c, — c, clockwise and counterclockwise rotation of organism** (observer in front); + c′, — c′, induced clockwise and counterclockwise movement of flagellum; *M* ?, possible southern migration of forms which have retained primitive rotation.

has received attention from several investigators, notably Delage and Herouard (1896), Goodspeed and Moore (1911), Bütschli and others.

There are several inferences of an axiomatic nature

that follow from such an hypothesis. Forms near the neutral equatorial region may be assumed to possess a slower rotation than forms near the poles and at the same time there may be expected to occur a change in the relative angle which the striæ make with the longitudinal axis of the body, their direction becoming approximately parallel with that axis. The cosmopolitan distribution of unicellular organisms with the evident non-selective value of the character makes such a hypothesis difficult of demonstration. The application of statistical methods would be of interest, however.

A second explanation of the rotation direction, apparently, however, a negligible one, is on the basis of the angular velocity of the earth so far as it may have an influence on small bodies at its surface. With free-swimming microorganisms oriented in accordance with the axis of the earth during definite intervals and rotating in the same direction that the earth rotates, conditions are fulfilled for such a mechanical explanation. When, however, the relative dimensions of the earth and the organisms as well as the relative density of the earth, the water and the organism, are considered, it is difficult to believe that the explanation lies in this direction. While many of the forms are attached to some definite surface in the water during certain periods of their development, there are others which reproduce directly in the water and should this have been the primitive condition of development, the rotation of the earth would have been ineffective.

While the possibility of electrical forces may be mentioned as an influence, there are no facts known which allow an interpretation in this direction.

During the past two years a considerable number of experiments have been made in attempts to obtain some definite evidence as to the cause of the rotation. Obviously it would be of interest to maintain a culture of northern forms in the southern hemisphere or a culture of southern forms in the northern hemisphere. Efforts

to obtain living cultures from desirable localities, the Falkland Islands, New South Wales, the southern part of South America, etc., have thus far failed. A method, however, was devised by which it seemed theoretically possible to subject northern flagellates to an environment similar to that of the southern hemisphere. A clinostat (Fig. 3) having a clockwise rotation of fifteen minutes

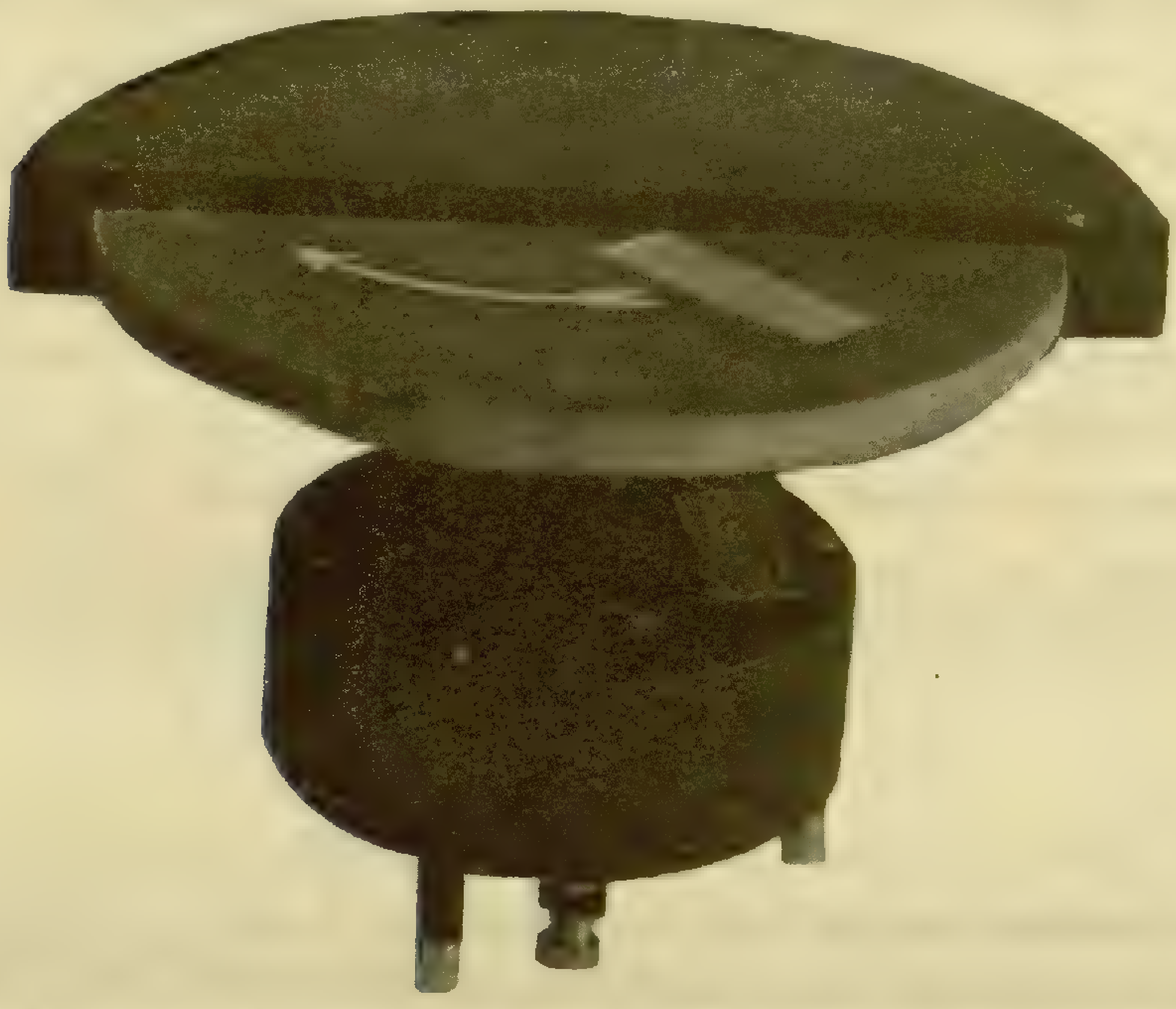


FIG. 3. A clinostat arranged for the purpose of subjecting northern flagellates, etc., to an apparent west east movement of the sun, the covered portion being toward the north.

was procured, a circular table ten inches in diameter fitted to this, and the northern half covered so that the revolving table containing slides in excavated recesses would pass into darkness on one side and emerge moving from east to west. Thus the apparent path of the sun so far as the organisms were concerned would be from west to east. The larger unstriated *Euglena* have been used almost entirely in the experiments, inasmuch as it would apparently be impossible to change the direction of rotation in forms like *Euglena spirogyra* Ehrenb., *Phacus pyrum* (Ehrenb.), etc., where the striæ are carinate in structure with an angle almost if not entirely precluding a rotation in the direction opposite to that in which they were accustomed to turn.

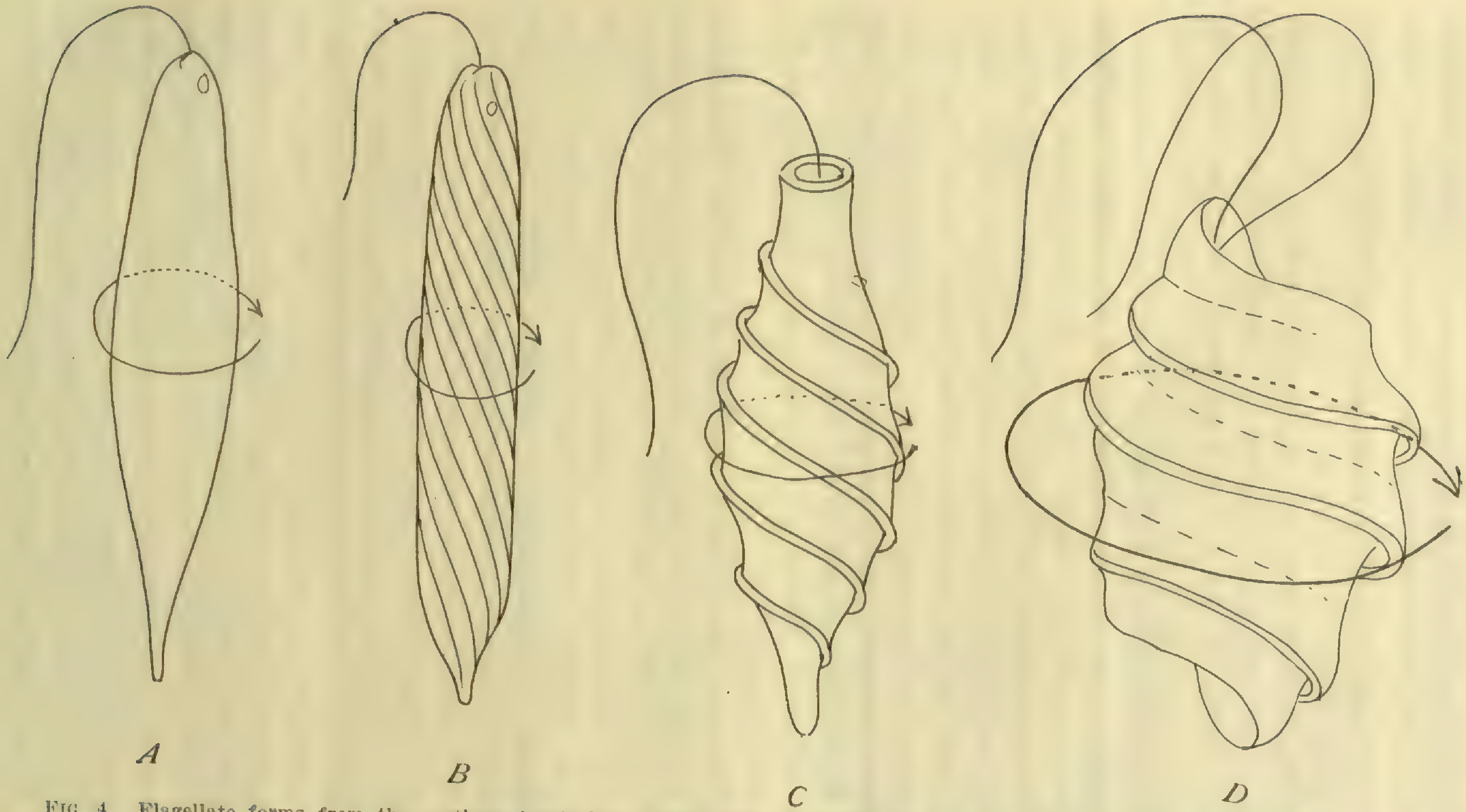


FIG. 4. Flagellate forms from the northern hemisphere illustrating the development of the left-hand striæ. *A, Euglena hæmogranulata* Walton (Ohio); *B, Euglena spirogyra* Ehrb. (Ohio); *C, Urceolus costatus* Lemm. (Europe); *D, Heteronema spirale* Klebs (Europe).

While there has been a large amount of data obtained, thus far no evidence shows that either a "reversal" or a "slowing up" of the rotation may be produced in any of the individuals utilized.

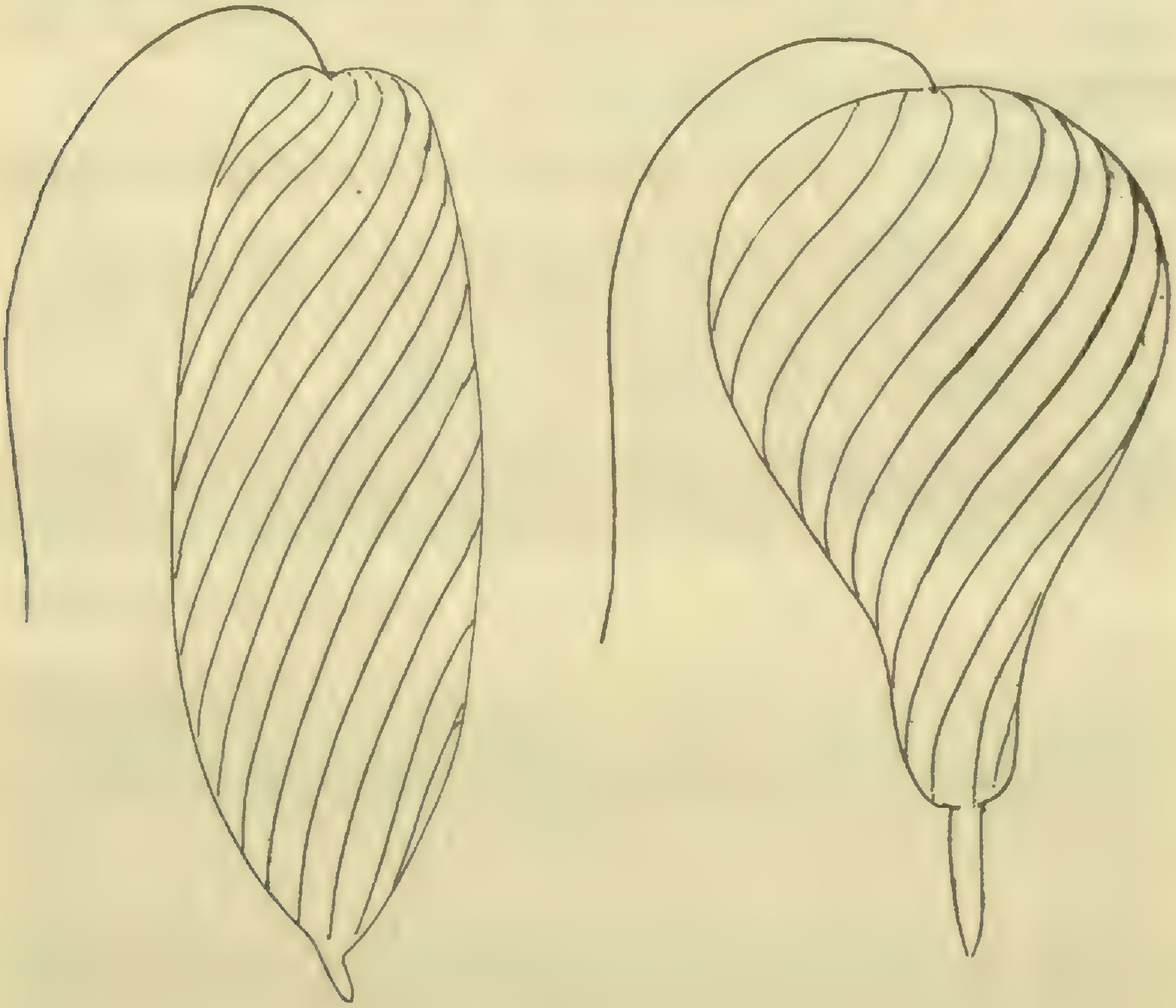
Even though it may not be possible to change the direction or the period of rotation in "adult" forms, may not such changes be produced in encysted forms or during a period when gametes are developed. Experiments are yet to be made with individuals in an encysted condition, and with material available it will be possible to utilize gamete-producing forms. That *Euglena* has a sexual cycle was pointed out by the writer nearly ten years ago (Walton, 1909).[7] Certain forms encyst, the cysts subdividing to approximately a 16-cell stage, small flagellate gametes emerge and conjugate. An experiment of this nature involves a discussion of the environmental effect on germ cells as compared with somatic cells, but does not affect the issues with which we are concerned in the present paper.

There are many other questions of interest which arise in a study such as outlined. For instance, what has been the origin of the striæ which are much specialized in many forms, although entirely absent in other forms (Fig. 4) so far as visibility with the microscope is concerned. The majority of the positive northern forms have "left-handed" striæ, a smaller number have longitudinal striæ, while a considerable number appear to have no striæ. None have been found with "right-handed" striæ. At first one may be inclined to attribute such a character to natural selection, but when one commences to ascertain the value of the character on the basis of progression, rotation and axial angle, such a conclusion seems less certain. There are a few facts that appear evident. First that the development of the striæ has been at a considerably later period than that of the rotation direction. Second that the relative position of the striæ has been largely dependent on the rotation. Third,

[7] Paper presented at annual meeting of Ohio Academy of Science, 1908.

that the development of the striæ has in many forms proceeded so far that a reversal rotation seems an impossibility.

The presence of a considerable number of other groups which have "left-handed" spirals so far as observation goes, is of interest. The various genera of Spirochætes, as well as *Spirulina* and *Arthrospira* among the *Cyanophycoidea* (*Cyanophyceæ*) may be mentioned. The twining of plants may, in the final analysis, be attributable to the same cause.



A *B*

FIG. 5. Flagellate forms from the southern hemisphere, Rio de Janeiro, Brazil (from Cunha), illustrating the development of the right-hand striæ. *A, Phacus bacilifer* Cunha; *B, Leptocinclis piriformis* Cunha.

Other related problems are the pendulation theory of Simroth (1912) relative to bipolar distribution, and the tropism theory as outlined by Verworn (1894), in connection with the excitation contraction of the flagellum.

V

Having indicated some of the difficulties existing along the lines of established research in the efforts to account for the derivation of the fundamental heritable units making up an organism and having presented a series of observations suggesting that a new perspective may be obtained by utilizing methods of attacking the problem somewhat different from those hitherto employed, the particular purpose of the paper is accomplished.

It may be asserted by some that such an attempt at a summary disposal of the existing evidence as to the actual origin of characters represents an unfortunate type of destructive criticism. Furthermore, that the acceptance of the validity of the arguments as to the long predetermined nature of the genes or subgenes, leads us once more in the direction of the somewhat antiquated theory of preformation. It is not impossible that these views are in part justified. Nevertheless it is well within the bounds of propriety to occasionally inquire as to whether the enthusiasm developed for a special discovery has not resulted in too broad an application of its principles. The mutation theory particularly as developed by Morgan is of interest. It is circumscribed at least in part by the phenomena of mendelian inheritance, and it is evident that one should look farther for the facts which may assist in explaining the real origin of the diversity of living things.

If additional studies support the view suggested by the facts here presented, namely, that characters of a physiological nature may be produced by environmental causes, and that these in turn may demand the correlation of morphological characters regardless of the origin of the latter, an important step will have been made in accounting for the primary differentiation of organisms. The later secondary differentiation through the combinations of units which have thus arisen, and which attains its maximum in the complex multicellular animals and plants, offers no particular difficulties in its explanation.

Furthermore, such an idea is more in harmony with the paleontological evidence as presented by Osborn (1912) and others, than one based on the mutational idea, and it is to fossil forms that one must look for the all-important historical record.

Should one propose a hypothesis of an ultimate unit, slightly plastic as to its immediate environment, but subject to the permutations and combinations of a mendelian type, and possessing a definite qualitative condition determined by prolonged environmental action, the picture is not at all so fanciful as some might at first thought insist.

The practical importance of such a viewpoint in its application to the problems of animal and plant breeding lies in the realization that new forms can not be created, but merely new combinations uncovered during the comparatively brief epochs of time which human intelligence has for working out the processes. Thus one returns to genetics.

In summarizing the paper, the following conclusions are suggested:

I. The heritable characters in general which make up an organism arise from preformed units in the nature of genes or subgenes that have been in existence during long geological periods of time. There are at present no criteria available in modern genetics by which an apparently new gene may be distinguished from one long in existence; furthermore, there is doubt as to whether new genes are actually arising in multicellular organisms. The change of a gene in a given direction, whether it be considered as a morphological unit or a chemical condition followed by the return to its original condition, suggests its composition of combinational sub-units, and is an argument against the idea that anything actually new has come into being during its series of so-called mutations. Such a conclusion receives additional support from the presence of apparently identical genes which exist in distinct species of organisms separated during

long epochs of time, as well as from the evidence of the non-contamination of genes during diverse environments.

II. The mutations demonstrated by DeVries and others, together with the variations obtained by Castle, are to be interpreted as a result of the combinations of existing genes. The mutations noted by Morgan and his associates, as evidenced from recurrence and stability, are in the nature of modal fluctuations having no definite cumulative value.

III. The direction of axial rotation in aquatic micro-organisms is best explainable on the basis of the apparent east-west motion of the sun having influenced the movement of the organs of locomotion. Thus the character becomes one acquired from external stimuli, and the persistence of reverse forms in both the northern and southern hemispheres indicates the hereditary nature of the character. Morphological characters, such as the striæ, etc., may arise in a similar manner or through selection. By correlation with the preceding characters, a cumulative and irreversible effect is produced.

IV. The primary factors in evolution are environmental and thus dynamic. The secondary factors of a combinational nature are gradually approaching a limiting maximum value, and are thus becoming static.

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SHORTER ARTICLES AND DISCUSSION

RHYTHMIC SYNCHRONISM IN THE CHIRPING OF CERTAIN CRICKETS AND LOCUSTS

SYNCHRONISM in the rhythmic chirping of the snowy tree cricket, *Œcanthus niveus* De G., has been observed and mentioned by a number of able observers, including Burroughs, Thoreau, McNeill and Dolbear. The synchronous chirping of this particular cricket has been too generally observed to be considered merely an illusion of the mind. In a previous paper[1] I reported that I had observed the occurrence of rhythmic synchronism in the chirping of colonies of the tiny tree crickets, *Cyrtoxipha columbiana* Caudell in Georgia. During the summer of 1917 I was afforded an excellent opportunity to make further observations of the synchronous chirping of these interesting arboreal crickets near Vinson Station, Virginia. A little colony had become located in the crown of a small black cherry tree in my back yard, where I could readily keep them under observation at all times. During the latter part of August, when the chirping season was at its height, a remarkable degree of synchronic rhythm characterized their chirpings during warm, quiet evenings. So constant was this rhythmic synchronism that only now and then would any irregularity occur. It finally occurred to me that I could subject their consecutive chirpings to a fairly accurate statistical analysis in the following manner. With a tablet of paper and a pencil I made a short horizontal dash for those instances when the chirpings were in unison, and a short vertical dash when they were not in unison. In this way I was able to record the consecutive chirpings for certain periods of time. In order to illustrate this method, I will give a graphic expression of the first period, which included 98 consecutive chirpings, 8 of which were not in unison.

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Fourteen different periods of consecutive chirpings were re-

[1] "Synchronism and Synchronic Rhythm in the Behavior of Certain Creatures," AM. NAT., Vol. 51, July, 1917.

corded in this manner, the results of which may be noted in the following table:

TABLE I

STATISTICAL ANALYSIS OF 14 DIFFERENT PERIODS OF CONSECUTIVE CHIRPINGS OF A COLONY OF CRICKETS OF THE SPECIES *Cyrtoxipha columbiana*

Period	Consecutive Chirpings Recorded	Chirpings in Unison	Per Cent. of Chirpings in Unison
First	98	90	91.8
Second	79	72	91.1
Third	85	72	84.7
Fourth	23	21	91.3
Fifth	78	72	92.3
Sixth	84	79	94.0
Seventh	66	59	89.3
Eighth	73	69	94.5
Ninth	45	44	97.7
Tenth	23	19	82.6
Eleventh	71	68	95.7
Twelfth	21	21	100.0
Thirteenth	75	74	98.6
Fourteenth	49	48	97.9
Total	870	808	92.8

From these data it would appear that out of a total of 870 chirpings observed, 92.8 per cent. were in unison. Even granting that some errors have been made in these determinations, it is quite evident that this observed high percentage indicates that a remarkable degree of synchronic rhythm occurs.

I kept this particular colony of four or five crickets under observation for a long time, and this rhythmic synchronism was always very noticeable. These crickets chirp most actively just before sundown. At this time every individual chirps briskly, and it is not long until chirping in unison is gradually established. This rhythmic synchronism does not take place at once, but becomes evident after the crickets have been chirping steadily for some time. When this rhythmic unison is fairly established it appears difficult for the crickets to chirp otherwise, for if there is any tendency toward asynchronous chirping, it is quickly overcome. A remarkable feature of the chirping of these crickets is a tendency now and then for the chirping to become noticeably accelerated briefly. Even though this occurs, the entire group keeps pace, so that the same unison is maintained.

The mole cricket (*Gryllotalpa borealis* Burm) is not an uncommon species in low grounds in this part of the country. Its notes

are low, mellow, intermittent chirpings—gur-r-r-r-r, gur-r-r-r-r, gur-r-r-r-r—which may be kept up almost incessantly during the active mating season. I have never been able to observe any definite rhythmic synchronism in the chirping of these burrowing crickets. However, late in August, during the season of 1918, I attempted an analysis of the notes of two of these crickets which were stridulating at the same time in their underground burrows in a wet spot near Vinson Station, Virginia. These two individuals chirped very persistently, and at times I noted some degree of synchronism.

TABLE II

STATISTICAL ANALYSIS OF 10 DIFFERENT PERIODS OF CONSECUTIVE CHIRPINGS OF TWO MOLE CRICKETS, *Gryllotalpa Borealis*

Period	Consecutive Chirpings Recorded	Chirpings in Unison	Chirpings Not in Unison	Per Cent. of Chirpings in Unison
First	46	30	16	65.2
Second	36	18	18	50.0
Third	62	36	26	58.0
Fourth	53	28	25	52.8
Fifth	28	16	12	57.1
Sixth	48	21	27	43.7
Seventh	37	14	23	37.8
Eighth	47	29	18	61.7
Ninth	21	10	11	47.6
Tenth	46	20	26	43.4
Total	424	222	202	52.3

From these data, which indicate that out of a total of 424 chirpings only 222, or 52.3 per cent., were in unison, it would appear that there was no particular tendency to maintain a definite synchronism in their chirpings.

The most remarkable instances of rhythmic synchronism I have ever heard have been afforded by the cone-headed grasshopper of the species *Neoconocephalus exiliscanorus* (Davis). A careful study of the intermittent notes—zeet-zeet-zeet-zeet—of these locusts was made on the edge of a swamp near Vinson Station, Virginia, late in August, 1917.

The characteristic habit of stridulation for individuals of this species is to produce a certain number of consecutive notes, followed by a brief pause. Usually, from fifteen to thirty consecutive notes are delivered before the pause takes place, then stridulation is again resumed. Rehn and Hebard[2] mention this habit as follows:

[2] Rehn, James A. G., and Hebard, Morgan, "Studies in American Tet-

The number of consecutive times without pause that this sound was produced were on one occasion counted, 26–14–20–20–17; usually on a warm evening an undisturbed singer would average about as above before ceasing a few seconds. The song is rapid, the sounds being emitted on warm evenings about 3 to the second.

When stridulation has become fairly established in a colony of these locusts, for the evening, it is likely to be continuous, for if some singers cease their notes briefly, others take it up. Rehn and Hebard, in the publication mentioned above, have also noted this behavior and say:

> When near a colony of this species on favorable evenings after dark the air is vibrant with the sound; as several singers cease others take up the constantly rising and falling song, but at no very great distance the song is inaudible.

In the colony observed by the writer at Vinson Station, Va., three individuals which were somewhat isolated from the rest maintained a perfect rhythmic synchronism for many minutes at a time, including in this period many hundreds of consecutive notes. Now and then all three would be stridulating at the same time, then only two would produce their notes, yet the same perfect rhythmic synchronism was always evident. Sometimes all but one would cease to stridulate, then one or both of the others would again take up the rhythm with a precision that was marvelous. It did not matter how often one or another individual joined the chorus following a pause, the notes were always perfectly synchronous from the start and the rhythmic synchronism was maintained.

A representation of this perfect synchronism which was evident as the different "singers" took up the rhythm from time to time may be shown graphically with dashes as follows:

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On several different nights I observed the same marvelous rhythmic synchronism in this particular group of individuals. Although other groups were "singing" elsewhere, it appeared

tigoniidæ: A Synopsis of the Species of the Genus *Neoconocephalus* found in North America, North of Mexico," in *Trans. Ent. Soc.*, 40, Jan. 6, 1915, pp. 365–413.

that their notes were delivered independently of the rhythm of this particular group. From observations of the stridulations of other groups in this same colony, I am of the opinion that it is not unusual for these locusts to develop a rhythmic synchronism in small groups.

It would be interesting to know why some species of locusts and crickets possessing the intermittent habit of stridulation tend to develop a more or less perfect rhythmic synchronism while others do not. Although this is true of the two crickets, *Œcanthus niveus* and *Cyrtoxipha columbiana*, I have been unable to note any synchronism in the chirpings of the common arboreal cricket, *Orocharis saltator*. Although large colonies of these crickets may often be heard in stridulation, each individual appears to stridulate in its own leisurely manner independently of its fellows.

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ON THE PIGMENTATION OF A CLYPEASTROID, MELLITA SESQUIPERFORATUS LESKE[1]

THE common clypeastroids, *Echinarachnius* and *Mellita*, when adult, are characteristically of a brown or (in the former species) reddish-brown color. This seems to be general throughout the group. Taxonomic lists contain, however, numerous references to a greenish coloration of the test of these animals. When preserved in alcohol, or when dried, either after fixation in alcohol or after killing with fresh water, these sand dollars usually assume, for a time at least, a somewhat greenish color. Clark (1899, p. 118) says that specimens of *Mellita sesquiperforatus* Leske (=*sexforis* A. Ag.) collected at Jamaica were delicate olive green [when alive, I infer, though with doubt]. He also gives the coloration of specimens of this species obtained in Porto Rican waters as "usually light olive green (rarely brown) when alive." At Bermuda living individuals of this species are, he says, invariably brown, with no hint of green about them, either on the external surface or in the viscera. When killed in alcohol, however, they become green, and greenish pigment is dissolved by the fluid. This is also true of *Echinarachnius parma* (Clark, 1904, p. 564; Coe, 1912, p. 111).

Now, examination shows that there is at the bottom of this

[1] Contributions from the Bermuda Biological Station for Research, No. 90.

matter—in descriptive lists somewhat confusing—a rather interesting point, which it is the purpose of this note to elucidate.

Mellita, adult, is at Bermuda undoubtedly brown; large specimens (9.0–11.5 cm. in transverse diameter, usually 9.5 cm.), which I have from time to time collected by dredging upon grass-free bottoms of fine sand or mud at Flatt's Inlet, Spanish Point, Two Rock Passage, and other localities, are uniformly brown upon both aboral and oral surfaces, although the different individuals vary somewhat as to shade. Their general hue harmonizes well with that of the substratum. It is improbable that light has had a direct effect in producing pigmentation, since the oral surface, never turned toward the light, is at least as densely pigmented as the aboral one and is frequently (in larger specimens) darker. Young individuals in an active, healthy state were gotten in association with adults during the autumn months. Up to 5 cm. diameter, in one case 8 cm., they were found, with one exception in about 30, to exhibit no brownish coloration whatever; they were, on the contrary, *pure white,* and translucent, the yellowish stomach being easily made out through the test. These individuals were usually 3.5 to 4.0 cm. in transverse diameter. The one exceptional specimen, 2 cm. in diameter, was unusual because it was of a light coffee-brown shade.

When placed in alcohol, or in fresh water, these young *white Mellitas* became bright green; in sunlight the green on alcoholic specimens quickly disappears. Clark (1901, p. 254) notes that some young specimens of *M. pentapora* examined by him were green [in alcohol?].

When kept in aquaria for several days the small white "sea-plates" developed, in most cases, local indications of green pigment, although the animals were still quite active. This was also true of the large brown individuals. It was noticed that in cases where a large brown *Mellita* had been damaged by the cutting edge of the dredge, a green coloration was present along the wound when the haul was brought to the surface. Other specimens, apparently uninjured, sometimes developed an olive-green color on the oral surface within half an hour after being transferred from the dredge to a tub of sea water.

Thus the green coloration of *Mellita* is associated with a condition of injury or death. It is possible that the green material may have no connection with the substance responsible for the general brown integumentary coloration of adults.

The green pigment is readily extracted with fresh water. It is not chlorophyll. When an animal is allowed to die in fresh water, the integument and the ordinarily white internal parts of the skeleton of a *Mellita* become bright green. Putrefactive changes decolorize the green extract, and the color can not be restored by alkali, or with H_2O_2. Green extracts are also decomposed, irreversibly, by boiling.

The green color is not seen in faintly acid fresh-water extracts and the *Mellita* remains brown. If such an extract is made alkaline, the green color promptly appears in the extract. The substance responsible for the green hue in dead or injured parts of *Mellita* is in fact a very good indicator. It is colorless in acid, vivid green in alkaline solutions; this color change may be reversed many times. The "turning-point" of the indicator is at an acidity of $p_H = 7.6$–7.8—in a solution more alkaline than neutrality, but well on the acid side of the reaction of sea water ($p_H = 8.1 \pm$). This greening material seems to be present throughout the body of *Mellita,* as freshly secured bits of the (white) internal skeleton turn bright green in alkali. The few available references to the coloration of clypeastroids indicate that the alkali-greening substance regularly occurs in *Clypeaster* and in other genera of this group.

The ovaries of *M. sesquiperforatus* are heavily pigmented by a substance of the "antedonin"-"echinochrome" group. The mature egg itself is light brownish yellow, heavily yolked, and apparently larger than any echinoid egg that has been described. It measures about 0.26 mm. in diameter, and is thus about twice the size of the egg of *M. testudinata* (=*pentapora*), which measures 0.11 mm., though not so large as that of the brittle-star *Ophioderma,* 0.30 mm. in diameter (Grave, 1916, p. 439). The ovarian egg of *M. sesquiperforatus* is surrounded by a gelatinous envelope, the whole being $0.35 \pm$ mm. in diameter. This envelope bears numerous evenly scattered clumps of precipitated reddish-purple pigment, the ovarian stroma being densely crowded with similar "chromatophores." In *Echinarachnius* the "chromatophores" of the egg-envelope are red rather than purple. The purple pigment of the *Mellita* ovaries exhibits the acid-alkali color changes and the absorption spectrum of the "echinochrome" pigments found in sea-urchins, holothurians, crinoids, and even in star-fishes; a dilute extract of a female *Mellita* may therefore be prepared which changes

from bright green to reddish purple at a hydrogen-ion concentration of about 7.5, the "echinochrome" not becoming orange until a much greater acidity is reached. This pigment becomes blue at an alkalinity of about $p_H = 8.2$; in the ovary it is reddish purple, but it is not in solution.

The interest of these facts lies not so much in their supplying some additional instances of the elaboration of similar (or even? identical) substances—conspicuously pigments—by animals related in descent, but in the evidence which is afforded regarding the reaction of intracellular fluids. Numerous cases illustrating the former point are available from among echinoderms, molluscs, tunicates, and so forth, and these cases have a certain importance for the general theory of animal coloration. But I am here chiefly concerned to point out that, if the alkali-greening substance present in *M. sesquiperforatus* is closely similar to that produced in the tissues of other clypeastroids, unequivocal statements as to the occurrence of greenish hues in living "sand dollars" may contain a suggestion as to a possible mode of origin for certain known geographical color differences in echinoderm species. I have not been able to find such references, but the point is worthy of further study. The evidence afforded by intracellular substances capable of behaving as indicators of acidity shows plainly that the tissues of marine animals are much more acid (less alkaline) than sea water. In *M. sesquiperforatus* the green color is produced when the tissue fluids become more alkaline than they customarily are; thus the integument, when injured or killed, becomes permeable to sea water and assumes a green hue. Healthy individuals for experimental work may, incidentally, be selected (at Bermuda) by the absence of green areas upon the test; the readiness with which greening is induced indicates the degree of care which must be employed in handling some marine animals. If by some means, for example, by higher temperature, the tissues of a *Mellita* population in a warmer sea were constantly maintained at a higher alkalinity than those at Bermuda, they might normally appear somewhat greenish in color. The normal variations in the coloration of *Chromodoris zebra*, a nudibranch containing an indicator favorable for such observations, strongly suggest that such differences in the reaction of intracellular fluids (not necessarily of the protoplasm) are entirely possible (Crozier, 1916). Whether or not comparable changes may be

induced as a regular thing in different oceanographic regions can not as yet be stated.

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PEMBROKE,
BERMUDA,
January, 1918.

W. J. CROZIER

A CASE OF ABNORMAL INHERITANCE IN DROSOPHILA MELANOGASTER

AMONG great numbers of cultures one is occasionally found which gives exceptional results not explainable by the usual mode of inheritance. Although such cases do not aid in understanding genetic problems unless the mechanism involved is worked out, the present case seems to be sufficiently remarkable to merit brief mention. The writer has no explanation to offer.

In culture 76, which was made up February 9, 1917, a large preponderance of males was observed, the ratio being 38 males to 3 females, and the males included unexpected classes. The parents of the culture were one homozygous eosin ruby forked female from stock and a male which was normal wild-type in all respects with the exception that the posterior cross veins of the wings were missing. His pedigree is unknown and he was

bred to determine whether the missing vein represented a genetic characteristic. This peculiarity probably had no relation to the exceptional nature of the offspring produced. The bottle was kept on the desk in the laboratory and the temperature was rather low most of the time, so that the larvæ developed slowly and the bottle became moldy before the flies finished hatching. It yielded exceedingly few flies, probably on this account as well as owing to the fact that nearly all the females were eliminated.

A count of the flies, as they hatched, gave 38 males and 3 females, a ratio which is inexplicable. The classes obtained were also as surprising. Owing to the cold the flies developed very slowly, so that the first offspring were removed on March 1 and comprised 18 eosin ruby forked sons. Four more hatched on the second and third, making a total of 22 eosin ruby forked sons which are of the expected class, since the three characteristics are sex-linked and the mother was homozygous for them. The count, continued until the thirteenth of March, gave a total of 3 normal females, which were expected in equal numbers with the males; 30 eosin ruby forked males; 2 eosin ruby males; 1 eosin male; 3 forked males; 2 normal or wild-type males.

The count in this case was kept up for more than the usual 10 days, but that could not have had any effect on the result in this case as no F_1 females were found until March ninth and could not have produced offspring, even had the temperature not been so low as to lengthen the incubation period beyond 13 days. The exceptional males, which are the cross-over classes ordinarily obtained in the F_2 generation from such a cross, could not be the result of a back-cross of the original mother to a son, as the only sons with which she could have come in contact were eosin ruby forked. In cases of primary non-disjunction, where sons inherit the sex-linked characters of the father, they inherit all his sex-linked characters, so that this can not be a case explainable by that means.

Contamination can hardly account for the results as the early males were of the expected class and later males always carried characters used in the cross, and the females were normal in appearance. Moreover, there is no known source of contamination that would give such a sex-ratio as this.

Results from the offspring were interesting but have not suggested any possible explanation of what occurred in the first generation. The eosin ruby forked sons were crossed out and

behaved quite normally in F_1 and F_2 generations. One forked son bred and gave offspring which behaved normally. The other two forked sons failed to produce any offspring, even though transferred to new bottles. The two eosin ruby sons were mated to bar females and afterwards rebottled with three females, but no offspring resulted. The eosin male also seemed to be sterile, as he was rebottled and remated without producing offspring.

The three daughters, which should have been heterozygous for eosin ruby and forked, and which have produced sons corresponding to that constitution, were crossed to brothers and gave the following unexpected results:

One in culture 88, mated to an eosin ruby forked brother, produced a total of 42 normal females, 74 forked females, 73 forked males, 37 normal males, and 13 eosin ruby forked males. A second in culture 93, mated to one of the wild-type brothers, produced 50 normal females and 28 forked females, 51 normal males and 73 forked males. The third daughter, mated to an eosin ruby forked brother, produced 2 normal, 35 forked, and 10 eosin ruby forked males; and 26 females all forked.

It is possible that the females were not virgin in these cases but that could not affect the sex-linked characters of the sons according to the normal mode of inheritance.

The two large classes of sons should have been the normal and eosin ruby forked classes, while the forked class of sons, which is the largest in all cases, should be no larger than the eosin ruby class, which does not occur even once.

Efforts to determine what was causing this abnormal inheritance were unsuccessful, because further breeding experiments showed the offspring of all classes to behave quite normally in all respects.

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